Age-Related Changes in ERPs Associated With Context-Based and Response-Based Interference

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Abstract

Age-related differences in information processing have often been explained through deficits in older adults' ability to ignore irrelevant stimuli and suppress inappropriate responses through inhibitory control processes. Functional imaging work on young adults by Nelson and colleagues (2003) has indicated that inferior frontal and anterior cingulate cortex play a key role in resolving interference effects during a delay-to-match memory task. Specifically, inferior frontal cortex appeared to be recruited under conditions of context interference while the anterior cingulate was associated with interference resolution at the stage of response selection. Related work has shown that specific neural activities related to interference resolution are not preserved in older adults, supporting the notion of age-related declines in inhibitory control (Jonides et al., 2000, West et al., 2004b).

In this study the time course and nature of these inhibition-related processes were investigated in young and old adults using high-density ERPs collected during a modified Sternberg task. Participants were presented with four target letters followed by a probe that either did or did not match one of the target letters held in working memory. Inhibitory processes were evoked by manipulating the nature of cognitive conflict in a particular trial. Conflict in working memory was elicited through the presentation of a probe letter in immediately previous target sets. Response-based conflict was produced by presenting a negative probe that had just been viewed as a positive probe on the previous trial.

Younger adults displayed a larger orienting response (P3a and P3b) to positive probes relative to a non-target baseline. Older adults produced the orienting P3a and

P3b waveforms but their responses did not differentiate between target and non-target stimuli. This age-related change in response to targetness is discussed in terms of "early selection/late correction" models of cognitive ageing.

Younger adults also showed a sensitivity in their N450 response to different levels of interference. Source analysis of the N450 responses to the conflict trials of younger adults indicated an initial dipole in inferior frontal cortex and a subsequent dipole in anterior cingulate cortex, suggesting that inferior prefrontal regions may recruit the anterior cingulate to exert cognitive control functions. Individual older adults did show some evidence of an N450 response to conflict; however, this response was attenuated by a co-occurring positive deflection in the N450 time window. It is suggested that this positivity may reflect a form of compensatory activity in older adults to adapt to their decline in inhibitory control.

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Abbreviations

ACC anterior cingulate cortex

BESA brain electrical source analysis

EEG electroencephalography

ERP event-related potential

fMRI functional magnetic imaging

HADS hospital anxiety and depression scale

IFC inferior frontal cortex

IFG inferior frontal gyrus

HAROLD hemispheric asymmetry reduction in older adults

MMSE mini-mental stat exam

PET positron emission tomography

PFC prefrontal cortex

SCOLP speed and capacity of language processing test

WM working memory

Introduction

Nearly every aspect of everyday living involves the selection of relevant information from a cluttered field of stimuli. Young healthy adults appropriately select beneficial streams from all potential inputs and ignore irrelevant streams with ease. This ability to select relevant inputs seems to be maintained later in life, however, the ability to ignore irrelevant stimuli appears to be compromised, increasing the distractibility of older adults (Anderson & Spellman, 1995; Hasher & Zacks, 1988). Despite general agreement on the qualitative observation of distractibility in older adults, there remains contention concerning its underlying neurocognitive basis. A variety of models and mechanisms have been posited to explain findings and generate predictions but no current framework offers a convincing enough account to produce a unified theory.

Hasher and Zacks (1988; Hasher, Zacks & May,1999) have proposed that a deficiency in older adults' ability to inhibit irrelevant items from entering and being maintained in working memory explains a considerable proportion of the variance associated with age-related decrements in cognitive functioning (Hasher, Chung, May & Foong, 2002; Lustig, May & Hasher, 2001; Hasher, Zacks & Rahhal, 1999; Kane, Hasher, Stoltzfus & Zacks, 1994). However, critics of Inhibitory Control Theory have noted that the definition of cognitive inhibition is still unclear and that inhibitory processes are not separable from alternative explanations of interference resolution, i.e., that simple increases in response time or error rates do not entail the presence of unique processes associated with inhibition (MacLeod, Dodd, Sheard, Wilson & Bibi, 2003).

Findings from imaging studies indicate that activation in inferior frontal cortex (IFC) is increased in response to interference in working memory and that anterior cingulate cortex (ACC) is active when inhibiting inappropriate response mappings (Nelson, Reuter-Lorenz, Jonides & Smith, 2003; see Figure 1). Nelson and colleagues interpreted this additional activity in ACC as representing unique interference resolution processes associated with response-based conflict, as opposed to separate familiarity-based conflict. Studies using older adults have thus far tested only the role of IFC in resolving interference in working memory (Jonides, Marhuetz, Smith, Reuter-Lorenz, Koeppe, et al, 2000) and have shown that older adults do not produce the specific IFC activity found in younger adults. This supported the notion that older adults have reduced capacities for inhibitory control. Unfortunately, while fMRI and PET imaging techniques offer excellent spatial resolution of active brain areas, temporal resolution is quite poor and this limits the understanding of *when* and *how* IFC and ACC contribute to inhibitory control processes. The focus of this thesis is to reproduce the behavioural findings of Jonides and colleagues (Jonides et al., 2000; Nelson et al., 2003) using a similar delayed-match-to-sample paradigm, and using high-density electroencephalography techniques to identify the timing of frontal lobe contributions to interference resolution.

Behavioural Studies of Distractibility in Older Adults

One of the first researchers to document age-related distractibility was Rabbitt (1965) who had younger and older participants categorize decks of cards marked with varying sets of stimuli indicating category membership. Rabbitt (1965) also varied the amount of irrelevant information on the cards, which was intended to complicate

categorization decisions. Older adults were as efficient as younger adults in sorting cards with either few (2) or many (8) relevant letter stimuli. An age-related difference did emerge, however, as the number of irrelevant letters on the cards increased from 0 to 8. As the number of distracters on the cards increased, the performance of older adults declined at a faster rate than that of younger adults.

Rabbitt (1965) concluded that this difference in performance was due to age differences in the number of display items that were sampled during target search by the older adults. He speculated that older adults attend to smaller samples of items than younger adults, increasing their overall search time. However, this shrunken sampling seemed to have been driven by increasing numbers of irrelevant rather than relevant items. For example, younger adults might sample 4 relevant items at a time to make category decisions, whereas older adults might sample 2 relevant and 2 irrelevant items. Rabbitt (1965) suggested that older adults had to reach a higher threshold than younger adults before disregarding irrelevant items; therefore, older adults were less likely to ignore the information from the irrelevant stimuli. Since only relevant cues could aid in performance, older adults' performance declined with increased numbers of irrelevant items.

There are at least two possible causes for this pattern of results. First, older adults may feel less sure about disregarding the distracters and, therefore, need more information to make their decision. This would lead to their processing goal-irrelevant stimuli that the younger adults would have already abandoned. The other possibility is that older adults could identify distracters as goal-irrelevant equally well as compared to the younger group but they have difficulty disengaging attention from

the distracters. This failure to disengage or inhibit the processing of distracters would clutter the contents of working memory and compromise processing of the target information. Rabbitt (1965) was one of the first researchers to suggest that this distractibility problem was due to decrements in inhibitory control.

Although Rabbitt's (1965) specific explanations for the pattern of results from this paradigm were not investigated further, the general finding that there was an interaction between age and distractibility became an important area of investigation in cognitive aging research. Attempts were also made to fit this "distractibility" problem into general theories of cognitive aging, such as Salthouse's General Slowing theory (Salthouse, 1988). Briefly, Salthouse (1988) proposed that the difficulties older adults experience from distraction results from a reduction in their speed of processing and, therefore, alterations in the temporal order in which specific elements of information processing are completed. For example, the decision process involved in identifying a visual stimulus as "irrelevant" may take longer in older adults compared to younger adults. If this delay were sufficiently long, sensory information may begin to degrade and could force some further processing to be necessary to react to the stimuli. Therefore, older adults would not have a problem with inhibiting stimuli, but rather a reduction in the efficiency of stimulus processing. The source of this slowing is further suggested to be caused by a reduction in general cognitive resources or "cognitive fuel" (Hartley, 1992). In cognitively demanding tasks, such as the Stroop task, controlling for speed of processing partially attenuated the performance differences between older and younger adults (Salthouse & Meinz, 1995).

Despite the usefulness of Salthouse's (1988) theory, residual performance differences between younger and older subjects consistently remained even after speed of processing was statistically controlled for. Examples of these residuals are described by Madden (1986; 1987) and show that when auditory target probes were presented to older and younger adults, the differences in response latencies were not sufficient to explain performance differences in several visual search tasks. Therefore, even with speed of processing controlled for, significant differences in visual search performance remained between the age groups.

Hasher and Zacks (1988; Zacks & May, 1999) also argued that the distractibility observed in elderly adults may be due to faulty inhibitory control. Their theory is similar to the explanation suggested by Rabbitt wherein the processing of non-relevant information affects behaviour. Hasher, Zacks and May (1999) argue that efficient information processing depends upon controlled attention and the management of working memory, such that goal-relevant stimuli are processed and non-relevant stimulus processing is restrained or suppressed. The mechanisms conceptualized to accomplish this are controlling *access* to working memory and the *deletion* of irrelevant items in working memory (Hasher et al, 1999)[1]. A failure to control access or to delete no-longer-relevant items will allow irrelevant stimuli to enter or remain in working memory.

The immediate consequence of this invasion into working memory is that, because of its limited capacity, the efficient representation and manipulation of relevant information becomes more difficult. In addition, occupying working memory allows irrelevant representations to receive sustained activation, and hence be

encoded into long term memory (Hasher et al., 1999; 1988). As a result, behaviourally relevant information is not encoded as efficiently as it normally would be, setting the stage for difficulties in accessing required information at a later time. This is particularly important during discourse comprehension in which an individual must rely on the "timely retrieval of information necessary to establish coherence among certain critical ideas" (Hasher and Zacks, 1988). Essentially, older adults with difficulties inhibiting the entrance of distracting information into working memory will have difficulties retrieving and acting upon behaviourally relevant information at a later time.

Hasher and colleagues' (1988) inhibitory control model of older adult distractibility has been applied frequently to discourse comprehension and speech, generating a considerable body of support: Older adults have more difficulty ignoring distracting text while reading in comparison to younger adults (Connelly, Hasher & Zacks, 1991). The elderly also show increased rates of intrusions of irrelevant information into speech (Gold, Andres, Arbuckle & Schwartzman, 1988) and are more likely to respond with considered but rejected words when forming sentence completions (Hartman & Hasher, 1991) or paragraph interpretations (Hamm & Hasher, 1992). Furthermore, models of working memory retrieval modeled as "conceptually focused selective attention" also support the importance of an inhibitory process and are consistent with the inhibitory control model (Anderson & Spellman, 1995; Gerard, Zacks, Hasher & Radvansky, 1991).

Hasher and colleagues' inhibitory deficit model has been met with great interest, as evidenced by numerous confirmatory tests found in the cognitive aging

literature (only a small sampling of which have been reviewed here). Indeed, cognitive inhibition is an intuitively appealing concept as it complements excitatory processes in allowing for more sensitive distinctions between internal representations of objects, as well as in aiding the selection of behaviours among competing response options (Houghton & Tipper, 1994). For these reasons, inhibitory models have become popular in explaining individual differences in information processing efficiency in healthy individuals as well as clinical populations including schizophrenics (Ellwanger, Geyer & Braff, 2003), Obsessive Compulsive Disorder (Aycicegi, Dinn, Harris & Erkmen, 2003) and children with ADHD (Mason, Humphreys & Kent, 2003).

Despite this support for the Inhibitory Control model, recent studies have presented specific criticisms of their inhibitory perspective. For example, Dywan and Murphy (1996) report on a discourse reading task in which young adults can avoid distraction better than older adults. Behaviourally, this seems to support the view that younger adults can inhibit the processing of task irrelevant information. However, after the task, both age groups were asked to identify those same distracter words in a test list. On this memory test, younger adults showed better memory for distracter items than older adults. If the younger adults were not allowing the distracter words into working memory (WM), then how were they encoded in long term memory and subsequently remembered? This line of research brings into question the *access* function of Hasher and colleagues' model, assumed to filter the items entering working memory. It is possible that younger adults do, in fact, process at least as much information as older adults, but are better able to control the amount of

processing allocated to that information and/or may be better able to control response tendencies.

Recent work on inhibitory control models of cognitive control attempt to deal with such critiques through a greater focus on specifying the neural location of such processes and better explaining the mechanisms whereby "inhibitory" effects are produced. For example, Braver and Barch (2002) propose a link between cognitive control systems involved in inhibitory control and context updating in working memory. Context is defined as any task-relevant information that could bias attentional selection or response patterns in the direction of fulfilling current behavioural demands. This would entail suppressing processing responses dependent on irrelevant or outdated information (Braver, Cohen & Barch, 2002). The importance of maintaining contextually relevant information on-line can be seen in a variety of tasks. For example, the Stroop task (Stroop, 1935) involves naming the ink-colour in which a colour word is printed (e.g., the word "red" coloured in blue ink). Maintaining these instructions in working memory is vital to biasing selective attention to processing and responding to the ink colour, and suppressing the automatic tendency to process the words (Braver & Barch, 2002). Maintaining context is, therefore, suggested as a module of working memory that regulates the representation of candidate information through early attentional selection or inhibiting processing of already represented content.

Braver and Barch (2002) suggested that the neural mechanisms supporting the context module of working memory are housed in dorsolateral prefrontal cortex (DLPFC). Furthermore, dopamine projections serve a regulatory role in modulating

PFC activity (Sawaguchi, Matsumura & Kubota, 1990; Williams & Goldman-Rakic, 1995), and are the hypothesized pathways by which context information is both maintained and updated. These sorts of models have opened new avenues with which to investigate the neural mechanisms of interference resolution by linking behavioural results to neurophysiology.

Neurophysiological Evidence of Inhibitory Control

Neurophysiological data have consistently supported an inhibitory control role for frontal cortices (e.g., Mecklinger, Weber, Gunter & Engle, 2003; Braver & Barch, 2002; Hazeltine, Bunger, Scanlon & Gabrieli, 2003; Miller & Cohen, 2001; Rainer, Asaad & Miller, 1998). Therefore, the extent to which cognitive resources are available in PFC to support inhibitory processes should predict the extent to which the processing of irrelevant stimuli may be suppressed.

Inhibitory suppression as modulated by resource availability in PFC was investigated in an fMRI study of working memory load, name recognition and face perception by de Fockert, Rees, Frith and Lavie (2001). Participants performed a selective attention task wherein names of famous people were identified, and faces, that may or may not match the name, were to be ignored. The task was further divided into conditions of high and low working memory load. A low memory load, for example, would be the five number sequence 6, 7, 8, 9, 10, while a high memory load would involve remembering a random set of five numbers, such as 6, 2, 4, 9, 3. A straightforward expectation from such a manipulation would be that as load increases there would be a decrease in the maintenance of the items held in working

memory as well as reduced processing of the name (Anderson, Reder & Lebiere, 1996). There are, however, two possible outcomes for the processing of distracter items. If participants are not actively suppressing the processing of the distracter face then increasing task demands (i.e., increased memory load) would limit resources available for stimulus processing and impair identification of face stimuli. However, a counterintuitive expectation would suggest that as processing resources are reduced, due to increased WM load, distracter stimuli would receive a greater degree of processing (de Fockert et al., 2001).

Results indicated that during high working memory load (and thus the disruption of inhibitory processes) a participant's ability to ignore distracter faces was reduced and there was increased activation in fusiform gyrus, an area thought to process faces (Hadjikhani & de Gelder, 2002). It seemed then that an active process (i.e., inhibitory suppression) was proactively suppressing the processing of the faces. However, as cognitive resources were reduced with increased load in WM, the ability to maintain that suppression of processing was reduced.

Such data offer compelling evidence that inhibitory processes can be selectively applied to the suppression of a non-relevant stimulus. Furthermore, prefrontal cortex appears to be critical for inhibitory processes, which are integrated into systems supporting working memory. However, some questions still remain. For example, can inhibitory processes be specifically applied to a single member of a stimulus set. In the de Fockert et al. study, inhibitory suppression was acting upon a separate processing stream than the targets, i.e., face perception versus name reading. What would be the result if two names were presented, one as a target and one as a

distracter? The obvious shortcoming to such an investigation would be that the same brain areas expected to show increased activity in processing the target would need to show decreasing activity for the inhibition of the distracter. For example, if the stimulus set used auditory presentations of words, then we would expect a target word to cause increased activity in secondary auditory cortex, while the suppression of a distracter word would slightly decrease activity in this area (Giraud, Kell, Thierfelder, Sterzer, Ruess, et al., 2004). Therefore, any reduction in activity from inhibitory suppression would most certainly be obfuscated by the processing of the target.

In re-examining the results de Fockert et al (2001), it should be pointed out that the alterations in stimulus processing or response selection resulting from conflict resolution processes should have been accompanied by a supervisory signal from cortical substrates in PFC (see Ridderkhof, van den Wildenberg, Segalowitz & Carter, 2004). Indeed, de Fockert and colleagues' results suggest that increased demand on frontal structures supporting working memory results in a failure to send a signal to fusiform gyrus to suppress processing of the faces. Therefore, identifying the activity in PFC that signals the need for inhibitory suppression would offer insights into the nature of such a function.

Neural Substrates of Prefrontal Cortex Supporting Cognitive Control

Bunge, Ochsner, Desmond, Glover and Gabrieli (2001) used fMRI to investigate the neural contributors supporting the maintenance of working memory load, and interference resolution in PFC. Participants were required to keep either 1, 4 or 6 letters in mind over a short delay and then indicate whether a presented probe

matched (positive probe) or did not match (negative probe) any letter in the target set. An interference manipulation was also done as a subset of the 4-letter condition, such that the current negative probe had been presented as a member of the target set on the just previous trial. This design was intended to reveal brain areas recruited for supporting increased WM load and, separately, brain areas involved in interference resolution. A variety of brain areas were activated during all conditions including bilateral dorsolateral and ventrolateral PFC, ACC, and parietal cortex. However, there were specific neural activations that correlation with interference resolution (left inferior frontal gyrus and right middle frontal gyrus) and load maintenance (anterior cingulate cortex).

These results suggested that there were no brain structures uniquely active only during interference resolution, but rather, integrated systems in WM provide added support during conditions of interference or increased load (Bunge et al., 2001). This was in contrast to previous findings supporting the specific role of dorsolateral PFC and parietal cortex in supporting interference resolution (Quintana & Fuster, 1999). However, Quintana and Fuster's (1999) study involved interference resolution specific to response selection rather than just maintaining the contents of working memory. This suggests that there may be separate systems supporting conflict resolution in working memory versus conflict resolution in response selection. Evidence from other research has supported a functional dissociation between these two processes. Filtering the contents of working memory is closely associated with ventrolateral PFC (Hazeltine, Poldrack & Gabrieli, 2000; Konishi, Nakajima, Uchida, Kikyo, Kameyama et al., 1999; Thompson-Schill, D'Espisito, Aguirre & Farah, 1997)

while the selection of task-relevant responses (through context-updating) is associated with dorsolateral PFC (Narayanan, Prabhakaran, Bunge, Christoff, Fine et al, 2005; D'Esposito, Postle, Ballard & Lease, 1999; Cohen and Servan-Schreiber, 1992).

In one recent study, Nelson and colleagues (2003) attempted to look at unique brain responses during context-based[2] and response-based interference resolution in working memory using fMRI. The task involved a modified Sternberg delay-to-match task in which participants judge a probe item as being part of a just previously viewed group of 4 letters. Interference resolution processes were recruited by manipulating the familiarity/salience of non-targets and thus requiring the resolution of non-informative familiarity through inhibitory processes. The difficulty of maintaining context information was manipulated by varying the familiarity of non-targets. This was done by presenting a negative probe item that was displayed in the four-letter target set of the immediately proceeding trial, similar to the method of Bunge et al. (2001). Also, response conflict was manipulated by presenting a positive probe from one trial as a non-target probe on the very next trial, creating a positive response tendency that needed to be overcome.

Imaging results indicated that interference resolution from the familiarity manipulation recruited left inferior frontal gyrus (IFG) while response conflict resolution additionally recruited anterior cingulate cortex (ACC) but with no additional IFG activation in comparison to high-familiarity trials. Nelson and colleagues (2003) concluded from their results that IFG and ACC make unique contributions to different aspects of cognitive control. According to some current theories of cognitive control, the ACC acts as a response conflict detector (Yeung,

Botvinick & Cohen, 2004), and that PFC (e.g., IFG) is recruited by signals from ACC to exert top-down control over processing by redirecting attentional resources and exerting cognitive control (Ridderinkhof et al., 2004). Although further research is needed to confirm the precise roles of ACC and IFG, their general role in maintaining cognitive control and exerting inhibitory suppression on stimulus representation and response selection is well supported. For the current discussion, the question now arises as to whether older adults show declines in the efficiency of processes supported by the relevant neural substrates.

Age-Related Changes to Interference Resolution

Considerable evidence has been gathered to suggest that the frontal lobes undergo dramatic neurological alterations with aging (Bunce, 2003). Neuropsychological investigations have indicated reductions in overall frontal cortex size, the number of neurons, the density of presynaptic terminals and the volume of blood flow feeding into the frontal lobe (for reviews, see Phillips, McPherson & Della Sala, 2002; Cabeza 2001; Raz, 2000; West, 1996; Lowe & Rabbitt, 1997). These neurological changes to the frontal lobe, specifically PFC, affect a wide variety of cognitive processes including language, decision making, planning, attention, and working memory (Damasio, 1998).

These alterations to the physiology of the frontal lobes have provided the basis for a growing body of research on the subsequent consequences of information processing in older adults, especially in terms of higher order cognitive processes such as memory and attention (Craik & Salthouse, 2000). If the healthy functioning

of frontal brain regions is disrupted, then inhibitory mechanisms associated with PFC could be disrupted with cascading effects on cognitive control and, therefore, behaviour. Specifically, this disruption is likely to reduce an individual's ability to withstand the interfering effects of distracting information.

Support for the idea that older adults have difficulty with inhibitory processes, because of the decline of processing efficiency in PFC, was found in a study by Jonides et al. (2000), using data from younger adults in a previous study (Jonides, Smith, Marshuetz and Koeppe, 1998). Jonides and colleagues (2000) investigated age-related differences in interference resolution of familiar but non-relevant stimuli using functional imaging techniques (conceptually similar to the singularly familiar condition later used by Nelson et al., 2003). However, as there was no specific response-related interference condition, there was no opportunity to view age-related changes in ACC activity. The resulting behavioural and physiological responses for younger adults (Jonides et al., 1998) were similar to those found by Nelson et al. (2003), showing activity in IFG for interference in working memory. Older adults (Jonides et al., 2000) performed more poorly than younger adults with respect to accuracy and RT. They also failed to show conflict-related processing in IFG. Jonides and colleagues (2000) suggested one possible explanation for these findings wherein IFG played a unique functional role in inhibitory processing.

However, other researchers using conceptually similar paradigms have found conflicting results. With regard to the dissociation between context interference and response conflict made by Nelson and colleagues (2003), a Stroop study by Milham, Banich, Webb, Barad, Cohen, et al. (2001) showed that while ACC does seem to be

particularly active during response conflict trials, inferior frontal cortex (IFC) is active under conditions of both non-conflict interference and conflict interference. That is, ACC seemed to play a unique role in response level conflict resolution, while IFG activity did not dissociate between different types of conflict (response level versus conceptual level). Furthermore, with respect to the age-related failure to show effects of interference in working memory, work by Dimitrov, Nakic, Elpern-Waxmen, Granetz, O'Grady, et al. (2003) showed that neither frontal lobe lesions nor early-stage frontal dementias seemed to have an impact on inhibitory processes during negative priming and stop-signal tasks. In order to deal with these incongruities in the imaging research, further work must be done to better understand the nature of the processes associated with context interference and conflict resolution. This should be done particularly with regard to the timing at which discrete brain regions become active under conditions of conflict.

Event-related potentials (ERPs), having fine-grained temporal resolution, would provide a complimentary approach to the imaging studies reported here and a further investigative step to this line of research. Electrophysiological research on attentional control in source memory tasks and cognitive control in the Stroop task can provide some insights into the neural responses that may be expected in such a task.

Event-Related Potentials Associated with Cognitive Control

Source memory tasks have been shown to be sensitive tools in identifying age-related declines in attentional control (Dywan, Segalowitz & Webster, 1998; Dywan, Segalowitz, Webster, Hendry & Harding, 2001; Dywan, Segalowitz & Arsenault,

2002). These source memory studies involved two phases: Phase one involved memorizing a study list of 25 words, each presented for several seconds. During phase two, participants were presented with a list of 125 words consisting of both the items from the study list and new words not seen before (foils). Some of the foil items were also repeated after a delay of 6 items, creating items with non-target salience (lures). Results from Dywan et al., (2003) revealed that both younger and older adults were equally skilled at identifying the target items and rejecting the singularly presented foil items, suggesting that older adults encoded the targets as efficiently as younger adults. However, the older adults were much more likely to mistakenly identify lure items as members of the target set, suggesting that the familiarity/salience generated from repeated lures interfered with their source memory. ERP responses on correct trials of the younger adults revealed a slow going, endogenous positivity over central-parietal sites in response to study items. This positivity, often referred to as a P3b or Late Positivity, was seen for target items but was attenuated for the foil or lure items. Analysis of the older adults' correct trials also revealed a P3b to study items, but not to foil items. However, unlike the younger adults, older adults produced a clear P3b for the repeated lure items.

Although the P3b has been linked to recollection in some studies (Herron, Quayle & Rugg, 2003) and familiarity in others (Johnson, Pfefferbaum & Kopell, 1985), the data of Dywan and colleagues (1998; 2001; 2002) reflected sustained attentional allocation. Younger adults seemed to be efficient in making an early discrimination between targets and non-targets, and appropriately allocating attention to the relevant items. The older adults seemed to be vulnerable to the increased

salience produced by lure repetitions. As a result, older adults allocated attention to these distracter items, even though they correctly identified them as non-targets (Dywan et al, 1998; 2000; 2002). This could be characterized as a failure to inhibit attentional allocation to the salient distracters. In summary, it appears that the P3b, at least in the context of source memory tasks, is sensitive to attentional allocation either for targetness or for a salient distracter. In relation to the paradigm used by Nelson and colleagues (2003), the P3b could be sensitive to selective attentional allocation by younger adults. If participants had difficulty in using task-relevant information to identify a probe as target or non-target because of salient irrelevant stimuli, then this would be reflected in a decrease in the differentiation of the P3b across conditions. Older adults, in particular, may have difficulty making efficient target identifications and may be likely to show similar P3b responses to both positive probes and salient familiar probes.

A great deal of research has also been conducted on electrophysiological responses during the Stroop task (Markela-Lerenec, Ille, Kaiser, Fiedler, Mundt et al, 2004; West, 2004b; Liotti, Woldorff, Perez & Mayberg, 2000; Rebai, Bernard, & Lannou, 1997). The work of West, Bowry and McConville (2004a) is particularly relevant because they studied varying levels of Stroop related conflict. They used a variant of the Stroop task based on digits, instead of ink colours and colour-words. In the Digit-Stroop task participants are presented with digits in a set of varying size (e.g. 2 2 2, 3 3 3, 1 1 1 1) and the task is to respond to the *number* of digits in the set. The set "2 2 2" would require a response of "3", for the three digits that were presented. However, the digit "2" in this example provides an incongruent cue to

respond "two". This is intended to mirror the interference generated from a colour-word failing to match and ink-colour in the traditional Stroop task.

West and colleagues (2004a) added an additional condition in which the incongruent probe either was an eligible response option or ineligible as a response option. For example, if digit sets ranged from one to four items, then presenting the set "7 7 7" provides a conflicting cue that does not have a response mapping. This distinction between eligible and ineligible Stroop trials provides a rough mapping onto the conditions used by Nelson et al., (2003): familiar trials are similar to the incongruent-ineligible Stroop trials as they involve contextual interference, while the incongruent-eligible trials are similar to the response conflict trials as they involve additional response interference.

The ERP component associated with these response-based and context-based interference trials is the frontal N450 (also known as the N400, but distinct from the semantic mismatch N400, e.g., Frishkoff, Tucker, Davey & Scherg, 2004).The role of the N450 has been suggested to be that of a general conflict detector, with possible neural generators in the ACC (Liotti et al., 2000; West et al., 2004a) and IFG (Markel-Lerence et al., 2004). The results of West et al. (2004a) showed a robust N450 to both incongruent-eligible and incongruent-ineligible trials, suggesting that the N450 was equally sensitive to both contextually-based conflict and, additionally, response-based conflict. Furthermore, they used source modelling techniques to show the neural generators of the N450 to be the anterior cingulate cortex and inferior frontal cortex. These data map well onto those of Nelson et al. (2003), who found context-based conflict to be associated with left IFG activity and response-based

conflict associated with activity in ACC, except that West et al. (2004a) did not associate the contributions of ACC only to response conflict trials.

Imaging studies have consistently indicated that ACC is uniquely active for response conflict (Botvinick, Braver, Barch, Carter & Cohen, 2001; Milham et al., 2001; van Veen, Holryod, Cohen, Stenger & Carter, 2004). West and colleagues (2004a) suggest that procedural differences may have resulted in this increased sensitivity of ACC to conflict trials on the whole because their procedure involved a high proportion of congruent and a low proportion of incongruent trials, therefore, increasing the salience of the incongruent trials. However, there have also been suggestions that ACC could be sensitive to conflict prior to the response selection stage (Botvinick et al., 2001) and that imaging findings have just been insensitive to such activity. It is possible that since the strength of the conflict in incongruent-ineligible trials may be weaker than the incongruent-eligible trials (Milham et al., 2001) that ACC response is reduced and, therefore, more difficult to detect. These speculations will require further study to fully clarify the sensitivity of N450 to the different varieties of conflict captured by these tasks.

One final point of interest comes from another study by West (2004b) in which the electrophysiological responses of younger and older adults were compared on a colour-based Stroop task, creating response-related interference (i.e., standard Stroop interference effect), while manipulating the difficulty of maintaining task context. These context demands were created by cueing the target stimulus before a trial began. For example, one cue would require a response to the colour word while another cue would require a response to the ink colour. This required constant

updating of the task context to allow for appropriate task switching. Comparing these trials to standard Stroop trials gave an indication of the task switching cost involved in updating the current context information held in working memory.

Behavioural results indicated that switching trials were more difficult for both groups but were particularly difficult for older adults, suggesting an added age-related difficulty in using context information from the cues. However, the important findings from analysis of ERPs showed that the latency of a frontal positivity around 300 ms following cue presentation was longer for older than younger adults. This was suggested to reflect the increased time required by older adults to encode context information. Also, the N450 components of older adults were attenuated in all but the most difficult trial types, i.e., those in which the incongruent switching trials where the ink colour was the target. West (2004b) interpreted these results as support for the notion that older adults have greater difficulty recruiting cognitive mechanisms to maintain task context and deal with response interference as a result of compromised dopamanergic pathways in PFC (Braver & Barch, 2002; Braver, Barch, Keys, Carter, Cameron, Cohen, Kaye, et al., 2001). With regards to the method of Nelson and colleagues (2003), the N450 could be sensitive to the specific activity associated with inhibiting irrelevant items held in working memory from previous trials (context-based interference in working memory) or the inhibition of prepotent response tendencies (response-based interference).The N450, therefore, may be relevant as an index of the activity found in inferior frontal gyrus and anterior cingulate cortex under response-conflict conditions.

The Present Study

The present study has been designed to investigate age-related differences in the relevant behavioural and electrophysiological factors as younger and older adults deal with familiarity-based context interference in working memory and additional response conflict, both factors tested in the context of a modified Sternberg task. In terms of behavioural results, it is hypothesized that both age-groups will have quite high levels of accuracy, as has been found in previous research (Nelson et al., 2003). However, it is expected that both younger and older adults will show small increases in response times and decreases in accuracy between baseline and conflict trials as the level of interference increases. Also, since older adults are likely to have more difficulty in resolving the conflict in interference trials, it is expected that there would be an interaction between age and condition, such that older adults will show greater interference effects than younger adults.

Two separate phases of analysis will be used to investigate differences in neural responses between age groups as seen in ERP responses. The first phase will focus on responses to perceived targetness as seen in the P2, P3a and P3b components. The P2 has been shown to reflect early stages of attention allocation and stimulus identification (Crowley and Colrain, 2004) and may be sensitive to a group difference in the efficiency of target identification in the present task. The size and latency of the P3a component has been suggested to reflect the updating of working memory following a behaviourally relevant stimulus (West, 2004b). Furthermore, as the current task requires the identification of probes into categories of "match" or

"mismatch", there may be a categorization effect in the P3a showing greater amplitudes for facilitated processing of targets than non-targets (Kok, 2001).

Stimulus categorization and context updating together may be expected to be more efficient in younger adults than older adults and would result in a greater differentiation between targets and non-targets in P3a amplitude and an overall shorter P3a latency for younger adults. The P3b is expected to reflect attentional allocation following target categorization and, in older adults, to be sensitive to the target salience (Dywan et al, 2002). In the present context, it is expected that both age groups will show enlarged P3b components to positive targets in comparison to the negative baseline. It is also expected that older adults will show enlarged P3b components to salient non-targets, as these trials will produce increased levels of both context-based and response-based interference for the older adults. That is, younger adults will be able to suppress their P3a/P3b response to stimulus repetitions that do not constitute targets within the context of the task.

The second phase of ERP analysis will involve the relation of the N450 component to conflict processing. Younger adults are expected to show N450 components of greater amplitude to interference trials and that the N450 amplitude should increase as a function of the degree of interference, with response-based conflict presenting the greatest challenge for response control. This would reflect the increased recruitment of inhibitory control processes by prefrontal structures (e.g., the IFG and ACC) in suppressing inappropriate response tendencies elicited by irrelevant context information (Nelson et al., 2003). In contrast, older adults are expected to show an attenuated N450 response to interference trials, which would reflect the

reduced efficiency in those neural systems involved in the suppression of irrelevant context information and response tendencies (Jonides et al., 2000; West et al, 2004b). Furthermore, the extent to which older adults can make appropriate behavioural responses to interference trials may be predicted by the amplitude of their N450 components.

Method

Participants

The tested sample consisted of 35 participants. One participant was excluded from all analyses due to technical difficulties during testing. Therefore, 16 young adults (6 male, 10 female) and 18 older adults (5 male, 13 female) were included in the analyses. Demographic data and the results of all paper and pencil tests are shown in Table 1. The younger group, ranging in age from 18 to 26 ($M = 20$, $SD = 1.9$), were recruited from an introductory psychology course at Brock University and received a combination of course credit and honorarium for their participation. The older group, ranging in age from 65 to 87 ($M = 74.3$, $SD = 7.3$), were recruited through newspaper advertisements from the local community and received an honorarium for their participation. The majority of participants were right handed (by self-report), while two younger adults and three older adults indicated left-hand dominance. The groups were equivalent in their educational history, $t(30) = .89$, *ns.*, with the older adults having an average of 14.8 years of education (range = 10-18 years, SD = 2.3) and the younger group having an average of 14.4 years (range 14-18years, SD = 1.0).

All participants completed a generic health questionnaire intended to gather information about both current health and past medical history. All participants reported no history of serious concussion, serious heart conditions or psychopathology. While the younger group did not report the use of any prescription drugs at the time of testing, the majority of the older group were taking prescription medications for hypertension (n = 14; 78%). With the use of hypertension

medications being typical in a population of older adults, including these 14 individuals was consistent with having a representative sample. One older adult reported having adult onset diabetes (type II diabetes), which was successfully managed through controlled diet.

Psychometric Measures

Spot-the-Word: Speed and Capacity of Language Processing Test (SCOLP). The SCOLP (Baddeley, Emslie & Nimmo-Smith, 1992) is a paper-based, forced-choice lexical-decision task intended to estimate verbal capacity. This measure was included to screen for general word knowledge differences between groups. The younger group had a mean raw score of 46.6 correct items out of 60 (SD = 4.6), which is lower than the older group, having a mean raw score of 52.1 correct items (SD = 4.7), $t(31) = -3.58$, $p < .001$. This difference in vocabulary skill is typically found when comparing younger and older adults and supports the notion that any age-related decline in performance on experimental measures should not be due to a disadvantage of the older group on basic verbal skills.

Hospital Anxiety and Depression Scale (HADS). The HADS (Zigmund & Snaith, 1983) was administered to all participants in order to gauge recent emotional state and to indicate any general emotional difference that could affect testing performance. The two age groups did not differ on the depression measure (M younger = 2.4, SD = 1.8; M older = 3.0, SD = 2.9), $t(32) = .90$, *ns*. However, the younger group did show higher scores on the anxiety measure (M younger = 7.1, SD = 3.6; M older = 4.6, SD = 2.2), $t(32) = 2.29$, $p = .05$. This difference on anxiety may be explained by the time of testing in that the majority of young participants took part

in the study within one week of the end of term exam period (mid-April). The purpose of the questionnaire was to ensure that the older adults did not have higher levels of depression or anxiety in comparison to the younger group. Therefore, any age-related decline in performance should not be due to elevated levels of anxiety or depression in the older adults.

The Trailmaking Test. The Trailmaking test (Reitan, 1979) is done in two sections on two 8½" by 11" sheets of paper. The "A" section is a timed task (recorded in seconds) and requires the participant to trace a continuous line from the numbers 1 through 25, which are randomly spread across the page. This is intended as a measure of basic perceptual processing speed, hand-eye coordination and motor control. The "B" section involves tracing a line through 26 alternating numbers and letters (1-A-2-B-3-C and so on) and tests the ability to alternate between sets, in addition to the processes tested in the "A" section. The difference in the amount of time taken to complete each section was calculated by removing the covariance between sections A & B. The residual score from section B was used as an index of executive functioning and showed that the younger adults performed better than the older adults on the executive functioning component of the task, $t(32) = 2.21$, $p = .034$. This finding is in line with literature suggesting a decline in executive function in older adults, potentially as a result of declining integrity of the frontal lobes (Bunce, 2003).

Mini-Mental State Exam (MMSE). The MMSE is a short neuropsychological test of cognitive status (Folstein, Folstein & McHugh, 1975) and can be used as a screening device to indicate the need for more comprehensive testing of symptoms that may indicate cognitive impairment. Participants from the older-age group

completed this measure with scores ranging from 27 to 30 out of a maximum score of 30 (M = 28.6, SD = 1.20). The expected normative scores for individuals in this age group is between 27 and 29, with a score of 26 indicating the need for further testing (Crum, Anthony, Basset & Folstein, 1993), thus suggesting the absence of any serious cognitive decline in the older group.

Procedures

The procedures reported here were part of a larger project and required the participants to attend two testing days. During the first day of testing, participants were greeted and escorted to the Brock University Neuropsychology Lab. After a brief description of the day's tasks, participants were asked to complete a consent form, health questionnaires and paper and pencil behavioural tests. During both testing sessions each participant's blood pressure was measured using a standard sphygmomanometer. Two electrodes were placed near the participant's left clavicle to record heart rate and an elastic respiration belt was fitted over their clothing to measuring breathing rate. Lastly, the participants were fitted with an electrode cap and seated in a quiet, dimly-lit, electrically shielded testing room. Each of the two testing sessions began and ended with a five-minute resting heart rate recording while the participant sat quietly with their eyes open. During the first day of testing, participants completed several flanker/item discrimination tasks as well as several verbal source memory tasks. During the second testing session participants completed a pro-saccade and anti-saccade task and a spatial memory test. The day also included a Sternberg item-recognition task using letters, the results of which are described here.

After completing both sessions, participants were debriefed regarding the purpose of the study.

Sternberg Delay to Match Task. In order to assess the ability to inhibit irrelevant context information and varying degrees of prepotent response tendencies, participants completed a variant of a Sternberg item-recognition task in which they made judgments as to whether a probe item was a member of a group of four just viewed target stimuli (See Figure 2). The procedure was based on the method used by Nelson and colleagues (2003). At the beginning of each trial, a fixation cross appeared at the center of the screen for 500 ms. Next, four lowercase letters (from the set: b, c, d, f, g, h, j, k, l, m, n, p, q, r, s, t, v, w, x, z) appeared in a box pattern around the position of the fixation cross. This display remained on the screen for 1500 ms. The probe appeared after a delay of 2000 ms and remained on the screen 1500 ms. The next trial began after a constant 2000 ms inter-trial interval. The entire session took approximately 45 minutes to complete.

The probe was a capital letter and was a member of the target set on 50% of the trails and was not a member of the target set on the remaining 50%. The participants responded by pressing a button marked "present" for probes from the target set and "absent" for probes not from the target set. Responses were counterbalanced such that half the participants responded "present" with the left hand and "absent" with their right hand; the other half used the reverse pattern.

The context-based and response-based conflict manipulations were made during the 50% of trials where the probe was not a member of the target set and took 4 forms: non-familiar non-target probes ("baseline trials"), familiar non-target probes

("familiar trials"), high familiar non-target probes ("highly familiar trials") and familiar, response-conflict probes ("response conflict trials").

Non-familiar, non-target trials were included to act as a non-target *baseline*. In this type of trial, the probe did not match any of the four stimuli in current or previous two target sets. On these trials one of the target letters from the preceding trial was repeated in the new target set, as seen in Figure 2 as the "k" in trial n-1 and trial n. This repetition was included to ensure that experimental trials differ from baseline trials only in that they require the resolution of the interference generated by context and response interference, rather than the presence or absence of repetition itself between target sets.

The *familiar* trials occurred when a non-target probe was presented as a target item on the immediately previous trial, but not the present trial. For example, a "b" may be a member of a target set on a particular trial, followed by an "H" probe letter. In the next trial the target set does not have "b" as a member but the probe letter is "B", requiring an "absent" response. However, the presence of the "b" in the target set of the previous trial confers a familiarity or salience to the "B" probe. This is thought to cause conflict in selecting and preparing the appropriate response: "absent". Any errors or increase in response time on this trial, compared to baseline, is considered to reflect the added difficulty involved in maintaining the proper context information and suppressing irrelevant context information from previous trials.

The rational of the *highly familiar*, non-target is similar to the *familiar* trials; the only difference being that a target "r" would have appeared in the previous *two* target sets rather than just one[3]. This is hypothesized to further increase the

familiarity or salience of the "R" probe and is thought to add to the difficulty of suppressing irrelevant context information.

During *response conflict* trials, the current probe ("H" for example) is not a member of the target set and, therefore, requires an "absent" response. However, on the previous trial, an "H" probe had elicited a positive response, as it was a member of the target set on trial n-1. This manipulation involved context-based interference as the negative probe on trial n was seen twice previously, once as a target and once as a probe on trial n-1. Nelson and colleagues (2003) suggested that the additional conflict resulting from the positive response to the "H" on trial n-1 would cause a prepotent response tendency that needed to be suppressed. Therefore, responses to *response conflict* trials should be quite similar to the highly familiar trial and any differences would likely be due to this added difficulty in inhibiting the previous positive response.

Also of note is the fact that each of the experimental conditions occurred independently (i.e., there was no overlap between the experimental manipulations of one condition and any element of the other conditions). For example, a total of three trials are associated with each highly-familiar manipulation: two priming trials and one lure trial. None of these three trials are associated with any of the manipulations of the other conditions. Likewise, none of the trials supporting the single familiar or response conflict conditions overlap with the conditions of any other trial.

The entire task consisted of 360 trials: 180 positive and 45 of each of the four types of negative trials. Since full trial randomization would not allow for the trial-to-trial carry-over effects required, the 360 trials were broken into 6 blocks of pseudo-

randomized trials. Participants completed 10 practice trials at the beginning of the task to ensure they understood the instructions.

Physiological Recordings

Electroencephalogram (EEG). EEG scalp data were recorded using a 256-channel Geodisic Sensor Net (Electrical Geodisics, Inc., Eugene OR; see Figure 3 for a graphical display of the electrode montage). The cap was fitted using skull landmarks (occipital protuberance, ears, nasian) and electrode sensors were individually adjusted to give the best contact with the participant's scalp. Impedances were maintained below 50 microvolts at the beginning of each separate task. Data were recorded (0.1 to 100 Hz bandpass, 500 samples per second) with a vertex reference and were converted to an average reference for analyses. Stimuli were presented using E-Prime research software (Psychological Software Tools, Inc., 2004) on a Dell VGA colour monitor 60 cm from the participant. Data were processed as 2200 ms segments with a 200 ms baseline. Trials containing movement artifacts were not included in the analysis. Trials containing moderate eye movements and blinks were corrected using a regression program created in Matlab studio (MathWorks, 2004).

Results

General Analysis

Following the hypotheses that have been laid out, the first analyses of neural responses were focused on distinguishing the effects of targetness from non-targetness through analysis of the P200, the P3a, and P3b components. Following this, the effect of interference in the different manipulations of the negative condition was examined through analysis of the N450 complex. During both of these analyses, age-related effects were investigated by comparing the behavioural and neural response profiles of both groups. A number of a priori comparisons had been planned, given expectations from previous research. However, as the present study is a replication of work done with fMRI and PET, and not EEG, the overall strategy of the present analysis is exploratory. Indeed, several of the analyses are strictly data-driven and are meant to generate hypotheses for future research. The analyses presented here have been corrected for violations of homogeneity of variance assumptions based on Mauchly's Test of Sphericity, wherever necessary, using Huynh-Feldt corrections for degrees of freedom. The original degrees of freedom are reported with the corrected F-statistics. Follow-up analyses employed Bonferroni and Tukey comparisons where appropriate. Refer to Appendix B for summary tables of statistical analyses.

Behavioural Data

Accuracy Data. The mean percentage accuracy for each condition of the Sternberg task is shown in Table 2 and illustrated in Figure 4. Accuracies for each condition by age group were entered into a 5 (condition) by 2 (group) Analysis of Variance (ANOVA). There was a main effect of condition, $F(4, 128) = 19.75, p$

$< .001$, $\eta^2 = .38$, and a trend for an effect of group, $F(1,32) = 4.06$, $p = .052$, $\eta^2 = .11$, with no interaction ($p > .30$). Follow-up analysis indicated that accuracy for the positive condition was lower ($M = .90\%$) than the baseline (M = 98%), familiar (M = 97%) and highly familiar (M = 94%) condition. The response conflict condition ($M =$ 91%) also had a lower accuracy than the familiar and baseline condition.

It appears then, from the accuracy data, that the positive and response conflict conditions caused difficulty for both age groups; however, the older group also found the highly familiar trials marginally more difficult than did younger adults. It is surprising to note that Nelson et al. (2003) found few significant differences between the different conflict trial types, considering that manipulations were intended to increase difficulty between conflict trials. Nonetheless, as the accuracy rate for every condition was quite high (the mean across all five condition is 93% accuracy in the older group compared to 95% in the younger group) there was no indication of any obvious deficits in the older participants' ability to perform the task.

Response Time Data. Response times for correct trials are presented in Table 3. As above, the condition by age group ANOVA showed a main effect of both condition, $F(4, 128) = 35.60$, $p < .001$, $\eta^2 = .53$, and group, $F(1, 32) = 17.12$, $p < .001$, $\eta^2 = .35$, with no interaction ($p > .45$). As can be seen in Figure 5, there is a constant effect of group, seen as a 200-275 ms delay in the responses of older adults in every condition. This is not surprising as research has shown that processing speed and raw response times decline during old age (Salthouse, 2000; Salthouse & Hedden, 2002). Therefore, it appeared that although older adults were slower overall than their younger counterparts, the effect of task difficulty was uniform over the two groups.

Follow-up analysis of conditions indicated that the positive (M = 877 ms), baseline (M = 932 ms) and familiar (M = 974 ms) conditions showed similar response times while the highly familiar (M = 1034 ms) and response conflict (M = 1057 ms) conditions had delayed responses in comparison to both the positive and baseline trials.

Results from response times complement the accuracy findings and further show that the conflict processing associated with seeing targets on previous, non-relevant trials did tend to increase difficulty for both groups. Interestingly though, the positive condition had the fastest response time in both groups while showing the poorest accuracy, suggesting a speed/accuracy trade-off. However, the response times for errors made in the positive condition were slower than correct response time (Young M = 948 ms; Old M = 1352 ms). If a speed/accuracy trade-off was present, then the response times for incorrect responses to the positive condition should have been faster than the response times for correct responses, i.e. errors would have resulted from premature responses. Instead, this pattern of correct responses to the positive trials might indicate a negative response bias, as errors tended to be made with prolonged response times. Perhaps the constant repetition of stimuli led participants to develop conservative response strategies such that they would doubt their memory for targets and have a bias to respond "not present". This could have increased accuracy for all four levels of the negative condition, but would have compromised performance on the positive trials. The exact source of this bias can not be clarified with the current data; however, recommendations for investigating such confounds will be discussed later.

Electrophysiological Responses

The ERP waveforms of the younger group for each condition at frontal-midline sites are presented in Figure 6a and Figure 6b. The P200, P3a, P3b, and N450 components were created from stimulus-locked ERP averages based on correct trials with a -200 to 0 ms pre-stimulus baseline. The P200 component is seen as a sharp positive deflection occurring around 200 ms after stimulus presentation, while the P3a is seen at approximately 300 ms over frontal sites and the P3b is seen as a slow wave at central-parietal sites from around 400 ms to 800 ms. As expected, the N450 is a more subtle negative deflection occurring between 400 and 500 ms post-stimulus and is actually seen as a discrete negative deflection that occurs during a large, slow negativity seen for every condition.[4] Figures 7a and 7b displays the corresponding ERP data for the older adults, and while a comparable P200 component is evident, the P3a and P3b components appear to be less differentiated between conditions. Furthermore, there appears to be no clear evidence of an N450 component. In fact, the waveforms of older adults appear to generally positive over midline sites, with the exception of site Fpz30. As will be discussed later, it is possible that a co-occuring positivity strongest at frontal sites, may reflect compensatory processes in the older adults to maintain their high performance (Grady, 2000; Gutchess, Welsh, Hedden, Bangart, Minear, et al., 2005). This will be discussed in further detail later.

The Effect of Targetness

The P200 Component. The P200 component, thought to reflect some aspects of attention allocation and perhaps an early stage of stimulus identification (Crowley & Colrain, 2004), was the earliest occurring component examined. The P200 was scored

by manually selecting the peak positive amplitude for each participant within a time window of 175 to 225 ms after probe presentation. These P200 peak amplitudes (presented in Table 4) were submitted to a 5 by 5 by 2 ANOVA with site (Fpz30, Fz15, Cz257, CPz100, Oz120) and condition (positive, negative baseline, familiar, highly familiar, response conflict) as the within-subjects factors and age group (old, young) as the between subjects factor. There was no effect of condition, F(4, 128) = .36, *ns*., no effects of group, $F(1, 32) = .73$, *ns*. The only main effect was for site, $F(4, 128) = 3.03$, $p = .032$, $\eta^2 = .09$, which can be seen from the waveform displays of brain activity in Figures 6a and 7a as a trend for the P200 amplitude to be greater at frontal sites. None of the interactions between condition, site and group resulted in any significant effects (all *p*-values > .10).

The results suggest that the P200 is not sensitive to the effect of targetness nor to the degree of conflict associated with the repetition of targets on previous trials. These results are notable, however, in that they show no differences between younger and older adults' neural responses during the early endogenous processing of a probe stimulus. Thus, any age-related differences observed in later components do not reflect an overall difference in EEG power, but rather age-related differences in the unique neural processes associated with a particular component and/or condition.

The P3a Component. The P3a component has been shown to be sensitive to stimulus categorization (Kok, 2001). For instance, a match between target and probe results in an increase in the P3a amplitude of younger adults (Zhang, Wang, Li & Wang, 2003). Working memory is updated following stimulus classification, allowing for the selection of relevant stimulus response mappings (West, 2004b). In the present study,

the P3a is considered to reflect the efficiency with which participants identify probe stimuli as targets (and thus allocate attention for further processing) or non-targets (and thus inhibiting the attention allocation). The average peak P3a amplitudes, made from the peak positivity found between 275 and 425 ms,[5] are shown in Table 5. The P3a components from sites Fpz30, Fz15, Cz257, Pz100 and Oz120 for each condition by each group were submitted to a 5 (site) by 5 (condition) by 2 (group) ANOVA. Although there were main effects of condition and site, these were superseded by interactions between condition and group, $F(4, 128) = 3.11$, $p = .026$, $\eta^2 = .09$, and site by group, $F(4, 128) = .3.82$, $p = .026$, $\eta^2 = .11$. There was, however, no main effect of group in this initial analysis ($p > .20$) suggesting that overall EEG power was not different between the two age groups.

A simple effects analysis of condition by site for each age group was done to further investigate these interactions. The younger group showed an effect of site, $F(4, 60) = 18.25$, $p < .001$, $\eta^2 = .55$, as well as condition, $F(4, 60) = 3.58$, $p = .012$, $\eta^2 = .19$, but there was no interaction between these effects ($p > .43$). It appeared from Figures 6 and 7 that the P3a was occurring maximally at frontal sites, particularly Fpz (see Figure 8), and so a planned comparison was carried out at this site to test the hypothesis that the younger adults' P3a component would differentiate the positive target probe from the negative baseline probe. A planned comparison using a correlated groups t-test at site Fpz supported this hypothesis and showed that the P3a was larger for the positive probe (3.47 μV) than the baseline probe (2.40 μV), $t(15) = 3.03$, $p = .008$. It appeared then, that even at this relatively early stage in processing, the younger adults were differentiating target from non-target stimuli. A further

analysis in the younger group was done to see if the P3a was sensitive to the effect of difficulty from the different levels of the negative condition. However, a repeated measures ANOVA of the four levels of the negative condition showed no differential effects on the P3a ($p > .33$), suggesting that the P3a was not sensitive to the manipulation of conflict processing.

The P3a amplitudes of older adults were submitted to an analysis of condition and site that resulted in a different pattern of neural responses from that of younger adults. The condition (5) by site (5) ANOVA resulted in only a trend for the effect of condition, $F(4, 68) = 2.40$, $p = .059$, $\eta^2 = .12^6$, but no effect of site nor any interaction between condition and site ($p > .30$). It appeared then, that the older adults did not show a reliably different response to positive probes compared to the non-target negative conditions. This finding is in line with the results from source memory tasks showing that older adults attend equally to targets and salient non-targets, while younger adults more resistant to non-target salience (Dywan et al., 2002).

One final analysis was done on the latency of the P3a. It was apparent when comparing the latencies of the P3a component in Figures 6a & 7a that the latency of the younger adults' positive peak is much earlier than the peak generated by the older adults. The mean latencies for each condition at site Fpz for the older and younger groups are presented in Table 6. These were submitted to a 5 (condition) by 2 (group) ANOVA. There was no effect of condition, nor an interaction of condition by group. However, there was an effect of group, $F(1, 32) = 84.49$, $p < .001$, $\eta^2 = .73$, such that older adults had an approximately 60 ms longer latency to the occurrence of their P3a component. This is consistent with literature suggesting that age-related changes in

the P3a reflect a reduced efficiency in older adults' ability to update the contents of working memory with relevant context information (West, 2004b)

The P3b Component. The P3b component is thought to reflect the continued allocation of attention towards a goal relevant stimulus (Dywan et al, 2002) as well as the processing involved in maintaining contextual information (i.e., following context updating) in the presence of conflicting stimuli (West, 2004b). The P3b was scored as the average amplitude from 400-800[7] ms across sites Fpz30, Fz15, Cz257, Pz100 and Oz120 (see Table 7). The average amplitudes were submitted to a 5 (condition) by 5 (site) by 2 (group) ANOVA. There was no effect of group ($p > .60$) again suggesting that, overall, the general neural responses of older and younger adults were of the same amplitude. There was an effect of site and condition; however, these main effects were qualified by a condition by site by group interaction, $F(16, 512) = 2.27$, $p = .044$, $\eta^2 = .07$. Each age group was analyzed separately to view the differential effects of site and condition.

The younger group's 5 (condition) by 5 (site) ANOVA produced a main effect of site, $F(4, 60) = 18.86$, $p < .001$, $\eta^2 = .56$, revealing that the P3b was showing the greatest positivities at more posterior sites, fitting with previous research (Dywan et al., 2002). The younger group showed an effect of condition, $F(4, 60) = 3.50$, $p = .012$, $\eta^2 = .19$. as well as a trend toward an interaction of site by condition, $F(16, 240) = 2.07$, $p < .059$, $\eta^2 = .12$, revealing that that nature of the condition differences changed when moving from frontal to posterior midline sites. This condition effect was further investigated through a planned comparison between the positive and baseline probe at site Pz, the maximal point of the P3b (see Figure 9). This

comparison showed that the younger adults produced larger P3b components to target stimuli (1.70 μV) than non-target baseline items (1.13 μV), $t(15) = 2.93$, $p = .01$. A one-way ANOVA of the different levels of the negative condition in the younger group showed that the P3b was not sensitive to the conflict inherent in these different trial types ($p > .67$).

The comparable 5 by 5 ANOVA in the older group failed to produce main effects of condition, site, or an interaction of site by condition (all p-values > .20). It seemed from this analysis that for the older adults, the P3b did not differentiate between any conditions, either for targetness or conflict processing. Furthermore, the P3b extended to frontal sites, whereas it was seen only in posterior sites in the younger group, which is typical of the hyperfrontality of neural responses that are often seen in older adults (e.g., Dywan et al., 1998). If the P3b does indeed reflect a continuous application of attentional resources, then while both age groups appeared to recognize the targets as seen in the P3a, only the younger adults showed signs of selectively applying attentional resources to the processing of the targets relative to non-target stimuli. The older adults showed an arguably less efficient response, such that attentional resources were allocated to target and non-target stimuli less discriminately.

The Effects of Conflict Processing

Localizing the N450 Component. The N450 was expected to differentially occur in response to the varying levels of the negative condition wherein non-relevant presentations of a current target on previous trials creates a prepotent response tendency to respond "present". As this effect was only expected in the negative

conditions, the positive condition was excluded from these analyses[8] but is displayed in tables and figures.

The N450 component was calculated as the average amplitude between 400 and 500 ms after probe presentation (see Appendix A for notes regarding the choice of this time window). These average amplitudes (see Table 8) were analyzed using a 4 x 4 x 2 mixed model ANOVA of frontal-midline sites (Fpz30, Afz21, Fcz08 and Cz257), condition (negative, familiar, highly familiar and response conflict) and age (younger versus older). The main purpose of this initial analysis was to identify the epicentre of the N450 component in each of the two age groups. As the N450 component is a robust yet relatively small component, the analysis included each midline site between Fpz30 and Cz257 in order to best capture the component. While there was no effect of site or condition ($p > .15$), there was a main effect of group, $F(1, 32) = 13.94$, $p < .001$, $\eta^2 = .30$. However, this group effect was superseded by a condition by group interaction, $F(3, 96) = 3.43$, $p = .022$, $\eta^2 = .10$. Figure 10 displays the amplitudes of the N450 along frontal-midline sites in both groups. The age by condition interaction is seen in that the older adults produced a similar positive response to the probe across conditions. In contrast, the younger adults produced an increase in the amplitude of their N450 to the probe as condition difficulty increases, thus showing a differential response across conditions. To summarize, the younger group showed a negativity that was sensitive to condition difficulty, an effect not observed in of the older adults.

A secondary analysis of lateralized sites (L38, AFz21, R03) was also carried out in order to investigate any changes in lateralized effects apart from the traditional

midline analysis (see Table 9). As has been suggested, a subgroup of generators for the N450 may be found in left frontal cortex (Nelson et al., 2003). This secondary analysis was to determine if lateral sites showed greater EEG power in the N450 than midline sites. Figure 11 displays the average N450 amplitude at site AFz21 and two lateral sites (Site03 and Site38). These data were submitted to a site (3) by condition (4) by age group (2) ANOVA. In line with the analysis of midline sites, the lateral sites showed no main effects of condition or site ($p > .15$), but did show a main effect of group, $F(1, 32) = 10.02$, $p < .001$, $\eta^2 = .29$. However, the group effect was qualified by an interaction of site by group, $F(2, 64) = 3.62$, $p = .039$, $\eta^2 = .10$. Follow-up analysis indicated that the age groups consistently differed at site AFz21, but did not consistently differ at the two lateral sites as younger adults ERPs tended to become less negative and the older adults' responses tended to become less positive as the site moved away from the midline. It appears from Figures 10 and 11 that the maximal amplitude from these three sites was occurring at AFz21. For this reason, further analyses were done at site AFz21, the apparent focal point of the N450.

The N450 at AFz21. Mean amplitudes of the N450 for each negative condition and age group are shown in Figure 12. These amplitudes were submitted to a condition (4) by age group (2) ANOVA. Similar to the analysis of frontal midline sites, there was no main effect of condition, $F(3, 96) = 1.86$, $p = .14$, *n.s.,* but there was a group by condition interaction, $F(3, 96) = 3.34$, $p = .022$, $\eta^2 = .10$, and an effect of age-group, $F(1, 32) = 17.67$, $p = .001$, $\eta^2 = .36$. Simple effects analysis were carried out within each age group and showed a main effect of condition in the younger group $F(3, 45) = 4.16$, $p = .011$, $\eta^2 = .22$, but no effect in the older group,

$F(3, 51) = .43$, $p = .74$, $\eta^2 = .04$. Figures 13-16 display the topographies across different conditions for each age group. Follow-up analysis revealed that the response conflict condition elicited a greater N450 amplitude ($M = -2.23$ μV) relative to baseline ($M = -1.06$ μV), with the context-based interference conditions falling between these extremes. This increased negativity in the N450 may reflect the increasing degree of interference across these response conditions. This is in line with the results of behavioural data showing the response conflict condition to have the lowest accuracy and longest response times of the negative conditions, suggesting the need for increasing levels of inhibitory control.

Exploring the Parameters of the N450. This failure to show any differentiation between conditions in the older group could have several explanations. One explanation for this lack of the N450 in the older group could be that the activity is simply not produced. A reduction in the ability to produce this component, due to underlying changes in cognitive processes required for these particular task demands, could be a natural result of aging. Indeed, West (2004b) suggested that the lack of the N450 in older adults is due to inefficiency in frontal brain areas associated with overcoming interference effects. If this were the case, it would be expected that the individual topographies of the older adults would be similar to the average topography of the whole group, and would lack negativities thought to be associated with the resolution of cognitive conflict. Figures 17 and 18 display the individual topographies for younger and older adults in the response conflict condition. The usefulness of the preceding analysis depended on both younger and older adults

consistently showing N450-related components across time (400-500 ms) and space (localizing around site AFz21).

As seen in the figures, fifteen out of sixteen younger participants (94%) showed some frontal negativity characteristic of the N450. Of these fifteen individuals, twelve displayed the N450 within the vicinity of site AFz21, thus giving rise to the effect of condition in the younger group. Similarly, thirteen of the eighteen older adults (72%) displayed some frontal negativity within the time window of the N450. However, only two of these participants showed negativities in the vicinity of the AFz21 site. With this high degree of variability in the location of these activities, it is not surprising that an individual midline or lateral site, such as AFz21, would not capture the variance associated with the N450 in the older group.

In order to deal with this issue, an exploratory analysis was carried out to identify the extent to which individuals from the different age groups showed neural responses in a consistent topographical location. This was calculated by identifying the discrepancies between the 3 dimensional coordinates of any individual's N450 component and the locations of the N450 from each peer in their age group (For a more detailed explanation of this calculation see Appendix A).

Maximal N450 Variance Distribution. The average variances of spatial distributions for the N450 measure are shown in Table 10. These data were analyzed in a condition (4) x age group (2) mixed model ANOVA and showed a main effect of both condition, $F(3, 96) = 5.20$, $p = .002$, $\eta^2 = .14$, and a trend for an effect of group, $F(1, 32) = 3.60$, $p = .066$, $\eta^2 = .10$. There was no interaction between condition and group ($p > .25$) suggesting that the two age groups showed similar decreases in site

variance (or tighter distributions of maximal N450 amplitudes) as trial difficulty increased. Follow-up analysis indicated that the effect of condition was mainly carried by the difference between the baseline and response conflict condition (see Figure 19). That is, as the need for response control increased, the clustering of the N450 components became tighter around the AFz21 site.

This tighter clustering of the N450 response around the AFz21 site could reflect an increase in top-down attentional control required as interference levels increased or as response-related interference arose. Indeed, all participants showed high rates of accuracy across all conditions, and so it would appear that neural responses became less variant with increasing task-demands. The important point here is that the older group did show a form of sensitivity to the level of conflict created by the more difficult trials. Although there was no effect of group nor any interaction, simple inspection of means for each group at the baseline and response conflict conditions showed, in fact, that older adults showed at least as great a decrease in site variance compared to younger adults. This sensitivity took a different form than would be observed through the typical analysis of negative amplitudes across sites, which had revealed only their lack of N450 related negativity.

Expanded Measures of the N450. The analyses conducted up to this point have indicated that the amplitudes of the younger adults' N450 components are sensitive to condition type, and secondly, that the spatial distribution of this negativity is influenced by condition difficulty. With this information in mind, examining the N450 response based on a clustering of sites surrounding site AFz21 may reveal more

stable differences between conditions and be more sensitive to condition type than would analyses based on a single site.

The values calculated from 400-500 ms post-stimulus presentation (see Table 11) were calculated by averaging the activities of 18 sites in the vicinity of AFz21 (see Figure 20). A condition (4) x group (2) mixed model ANOVA revealed an effect of age group, $F(1, 32) = 7.74$, $p = .009$, $\eta^2 = .20$, and a trend for condition, $F(3, 96) = 2.30$, $p = .081$, $\eta^2 = .067$, superseded by an age group by condition interaction, $F(3, 96) = 3.12$, $p = .032$.

Simple effects analysis of data from the younger group supported the condition effect, $F(3, 45) = 3.98$, $p = .014$, $\eta^2 = .21$, whereas the older group showed no differentiation among conditions ($p = .76$). Follow-up analysis in the younger adults revealed that response conflict condition (-1.82 μV) differed from both the baseline (-0.46 μV) and highly familiar conditions (-0.91 μV) (see Figure 21). Of note was a difference between the baseline condition and the familiar condition (-1.39) which was not evident in the single site anlysis. Thus, a wide-spread sampling of the N450 appears to be more sensitive to condition type, an option only possible with the recent use of high-density electrode montages (e.g., Markela-Lerenc et al., 2004; West, 2004a).

Relationships Between ERPs and Behavioural Measures

An analysis was carried out to investigate relationships between behavioural measures and ERP components[9] (see Table 12). It was thought that the residual of the Trails B, the unique variance remaining after controlling for covariance with the Trails A score, as well as the accuracy and response times from the response conflict

trials would relate to information processing efficiency and, therefore, correlate with their targetness and interference related ERPs[10]. However, correlation analyses provided no support for these relationships. The accuracy and response time measures may not have been well predicted by the ERP responses because participants managed to maintain high levels of behavioural response in the face of considerable variation in neural responses between conditions and groups.

A further analysis was also done to investigate interrelationships between ERP components from the positive, familiar and response conflict conditions. In order to control for baseline confounds in the ERP components the shared variance between each interference condition and the baseline condition was removed. This left a residual of the unique variance from each of the interference conditions. The correlations are shown in Table 13. First, it was thought that the P3a and P3b components may relate to each other as they are both thought to be sensitive to the targetness, or salience, of a stimulus. The younger group showed evidence of a relationship between the P3a and P3b in the Positive condition, r(14) = .50, p = .049 (see Figure 22a), familiar condition, $r(14) = .704$, $p = .002$ (see Figure 22b), and a trend for a positive relationship in the response conflict condition, $r(14) = .480$, $p = .06$ (see Figure 22c). It seemed then, that the initial response to the stimulus predicted subsequent attentional allocation in the younger group. The older group showed a relationship between P3a and P3b components only in the positive condition, r(16) = .487, p = .044 (see Figure 23).

The correlations between the P3a and P3b and the N450 revealed an interesting dissociation between relationships with the P3a and P3b. The younger group showed

evidence that the P3b was related to N450 activity in the familiar condition, $r(14) = .796$, $p < .001$ (see Figure 24a) and the response conflict condition, $r(14) = .731$, $p < .001$ (see Figure 24b). This suggested that a withholding of attentional resources in the conflict conditions, as seen as a reduced amplitude of the P3b, corresponded to greater inhibitory control, as seen as a stronger negativity in the N450. Although the older adults did not show a relationship between the P3b and the N450, they did show a consistent relationship between the P3a and the N450 in the familiar condition, $r(16) = .724$, $p = .001$ (see Figure 25a) and response conflict condition, $r(16) = .520$, $p = .027$ (see Figure 25b).

The failure to relate the P3b with the N450 may be a result of older adults' difficulty in modulating the attentional resources applied to the probe, as evidenced by the undifferentiated P3b response. However, the relationship between the P3a and the N450 may suggested that, to the extent that older adults were able to properly discriminate non-targets from targets, as evidenced by a suppressed P3a response to non-targets, they showed some evidence of the N450. However, it is also possible that the P3a of the older adults could be related to the diffuse positive activity seen in the N450 window. If these diffuse frontal positivities are evidence of compensatory activity, for example, then this may have resulted in a positive relationship between the cognitive resources being applied in the P3b as well as additional frontal resourced recruited during the N450 window. However, it is conspicuous that the P3a of the younger adults did not show any evidence of relating to the N450. Further study will be needed to fully investigate these relationships.

Preliminary Source Analysis of the N450 in Young Adults

Imaging studies have shown unique neural activity associated with the suppression of irrelevant context information and the inhibition of response tendencies to occur consistently in inferior frontal cortex and anterior cingulate cortex (Nelson et al, 2003), respectively. Source analysis of the neural generators of the N450 in the Stroop task have also consistently shown a prominent role of both inferior prefrontal cortex and anterior cingulate cortex in overcoming the interference in incongruent trials (Liotti et al., 2000; Markela-Lerenc et al., 2004; West et al., 2004a). Brain Electrical Source Analysis (BESA, version 5.1, Megis Corporation, 2004; for an example analysis see Kiefer, Marzinzik, Weisbrod, Scherg & Spitzer, 1998) was used to investigate the neural generators of the N450 during the Sternberg task. As the older adults did not produce recognizable N450 components as a group, these preliminary analyses were restricted to the neural responses of younger adults.

A typical procedure used for identifying the unique generators of the N450 in the Stroop task involves constructing a difference wave by subtracting the congruent condition from the incongruent condition (Markela-Lerenc et al, 2004). However, although the Sternberg task involved both positive and conflict trials, it is arguable as to whether a difference wave based on these two conditions would be comparable to the difference wave created in Stroop tasks. Also, there appeared to be unique activity seen in the positive and baseline conditions and not the conflict conditions that, if a difference wave was made, would actually introduce noise into the residual difference wave and thus difference waves can be misleading (e.g., van Boxtel, 2004). For this

reason, preliminary dipole models were generated for the whole condition averages and not the difference waves.[11]

Source models were based on responses for the positive condition, baseline condition, negative familiar condition (because it appeared to exert a more robust effect than the negative highly familiar trials), and the response conflict condition over a time window from 400-500 ms post-stimulus onset (see Figure 26). The dipole model for the positive condition (see Model 1) indicated a primary generator in left superior parietal cortex (Cartesian coordinates: x = -26.9, y = -9.0, z = 75.2). Secondary generators were best fit by two symmetrical dipoles in left and right inferior prefrontal cortex (Cartesian coordinates: right hemisphere dipole, x = 24.5, y = 51.5, z = 32.4; left hemisphere dipole, x = -24.5, y = 51.5, z = 32.4). The model proved to be a good fit to the data (residual variance of 8.5%) with the first dipole showing its maximal dipole moment strength at 440 ms post-stimulus and the secondary dipoles at 490 ms post-stimulus.

The baseline condition (see Model 2) showed a primary generator in right superior parietal cortex (Cartesian coordinates: x = 24.1, y = -14.7, z = 76.9) and secondary generators in bilateral inferior frontal cortex (Cartesian coordinates: left hemisphere dipole, x = -30.5, y = 46.1, z = 26.3; right hemisphere dipole, x = 30.4, y = 46.1, z = 26.3). The model showed a relatively good fit to the 400-500 ms window (residual variance 11%) with both the superior parietal and inferior frontal generators showing maximal dipole moment strengths at 420 ms post-stimulus.

The dipole model of the familiar condition (see Model 3) showed a pair of symmetrical generators in inferior prefrontal cortex (Cartesian Coordinates: left

hemisphere dipole, x = -35.9, y = 43.1, z = 26.6; right hemisphere dipole, x = 35.9, y = 43.1, z = 26.6) and a secondary generator in left anterior cingulate cortex (Cartesian coordinates: x = -7.8, y = 58.2, z = 67.5). The model showed a reasonable fit (residual variance 15%) with the inferior prefrontal generators showing maximal dipole moment strengths at 405 ms post –stimulus and the anterior cingulate generator at 425 ms.

The dipole model for the response conflict condition (see Model 4) was quite similar to the familiar condition with symmetrical dipole generators in inferior prefrontal cortex (Cartesian coordinates, left hemisphere dipole, x = -36.3, y = 43.2, z = 26.6; right hemisphere dipole, x = 36.3, y = 43.2, z = 26.6) and left anterior cingulate (Cartesian coordinates: x = -7.8, y = 58.2, z = 67.5). The model had a relatively good fit (residual variance 12%) with the inferior prefrontal generators showing a maximal dipole moment strength at 430 ms post-stimulus and the anterior cingulate generator at 460 ms.

The validity of each of these models was tested first by attempting to fit additional dipoles in the 400-500 ms window; however, no additional dipole could account for more than 2 or 3 percent more variance, suggesting that no additional brain areas were contributing to the activity within the window. Additional bilateral dipoles were fitted for the ACC and posterior parietal generators; however, including these additional dipoles did not improve the model's fit, suggesting that the single dipoles were not midline accommodating two underlying generators in more lateral positions. Each generator site was also tested by moving each dipole in each model

several x, y and z units in the positive and negative poles, but this did not improve the residual variance fit by more than a fraction of 1% in any condition.

The dipole models constructed here were consistent with evidence from imaging work with the Sternberg task by Nelson and colleagues (2003) suggesting key neural generators in IFG and ACC. The present source analysis is also consistent with the findings of Markela-Lerenc and colleagues (2004) who found that inferior prefrontal activity associated with the N450 preceded ACC activity.

Discussion

The notion of compromised inhibitory control in older adults has been an alluring framework to cognitive-aging research over the past two decades (e.g., Anderson et al, 1995; Hasher et al, 2002; but see MacLeod et al, 2003). Altered inhibitory control functioning, conceptualized as an aspect of general cognitive control, has the potential to explain a large portion of the variance associated with age-related changes in executive functioning, memory, attention and response control. Specifically, the inhibitory control theory of Hasher, Zacks and colleagues (1988, 1999) has gathered a great deal of experimental support in recent years from behavioural paradigms. In addition, new avenues of investigation have been opened by the use of physiological techniques, including imaging (e.g., de Fockert et al, 2001) and electrophysiological methods (e.g. West et al, 2004a), in order to investigate the *why* and *how* of age-related inhibitory control changes in older adults.

The primary question addressed in this study was whether older adults experienced greater response interference effects than younger adults when dealing with conflicting stimuli. Also at issue was whether differences in the neural responses of younger and older adults would offer insights into the nature of inhibitory control processes in the two age groups. Jonides and colleagues (1998; 2000) investigated this issue using functional imaging and found that interference from old target sets resulted in unique activity in inferior frontal cortex. The researchers suggested that these unique neural responses could be related to the inhibitory control processes required in the task. However, the specific nature of the contributions from these brain regions largely remained unknown.

The present study was conducted in order to extend the findings of Nelson et al. (2003) and Jonides et al. (2000) using high-density EEG recordings in order to identify the specific time course of inhibitory control processes engaged by the task. ERPs were collected as younger and older adults were required to respond "present" to target stimuli and "absent" to non-targets in a modified Sternberg task. Varying task demands in the target absent condition allowed for the investigation of the effects of conflict induced by the familiarity of the probe stimuli or, additionally, by a prepotent response tendency.

It was expected that as the potential for interference increased, response speed would increase and accuracy levels would decrease compared to the baseline condition. Electrophysiological results had two complimentary focus points wherein initial target identification, as seen in the target specific P3a, was expected to set the stage for subsequent discrimination of target events as observed in the differential amplitudes of the P3b and N450. ERPs elicited during target identification were expected to show that younger adults made efficient early responses to targets and inhibited further processing of all non-targets, while older adults were expected to show a less-differentiated neural response to these stimuli.

Behavioural Outcomes. The behavioural data from the Sternberg task was generally in line with previous research using the same or similar paradigms (Nelson et al., 2003; Jonides et al., 2000). There was a difference between the positive and negative baseline condition, such that both younger and older adults were more likely to make false negative responses to positive targets than false positives to the baseline condition. Although the positive condition showed the poorest accuracy and the

response times to correct trials in this condition was faster than the other conditions, this pattern did not appear to be a result of a speed/accuracy trade-off. Response times on errors for the positive condition were slower than to correct, supporting the notion of a negative-response bias. This negative response bias likely inflated the number of correct responses to all non-targets. A cautious response strategy may have been adopted by the participants as they became aware that many of the negative trials were luring them towards making a false positive response.

The conflict manipulation resulted in a pattern of declining accuracy from the negative baseline condition to the response conflict condition, but with little apparent differentiation in the baseline and familiar conditions. These increasing error rates in the familiar and response conflict trials are thought to be a behavioural cost associated with the interference generated by familiar stimuli and incompatible stimulus-response mappings from previous trials (Nelson et al., 2003). However, the overall pattern of performance was quite high for both groups, averaging over 90% correct in most conditions. Therefore, the neural responses associated with each condition and group, being based only on correct trials, reflects a response profile that led to successful response selections in both younger and older adults.

Response time data showed a similar condition effect and also appeared to show a rather dramatic effect of age-group with a nearly uniform 200 ms increase in response times in older compared to younger adults. However, if older adults have more difficulty dealing with the interference generated from irrelevant stimuli, then they would show additional accuracy and response time costs as interference effects increased. While the reliable 200 ms difference does confirm an effect of general

slowing in the older adults (Salthouse, 1996), there did not appear to be a different pattern of interference effects between the two age groups. Instead, the behavioural data are best characterized as showing clear effects of interference-related difficulty but, after controlling for general slowing, the responses of older adults followed a relatively similar pattern to that of younger adults with respect to the behavioural consequences of the interference manipulations.

Other lines of research have found similarly intact performance in older adults during simple working memory tasks. For example, Oberauer (2001) compared younger and older adults' behavioural performance on tasks dissociating interference effects in long-term memory from immediate interference effects in working memory. He found that older adults showed age-related declines in their ability to inhibit items encoded in long-term memory but showed comparable behavioural performance when immediate suppression was required in working memory. This is not to say that older adults go about the task in the same manner as younger adults; however, as indicated in this study and in the work of Oberauer (2001), older adults are able show nearly equivalent behavioural performance after accounting for the effects of general slowing.

Electrophysiological Response to Targetness. In the present study, the effects of targetness were investigated by comparing condition and age group effects on the P200, P3a and P3b. As the P200 component is thought to reflect only an early stage of stimulus identification (Crowley & Colrain, 2004), it was not surprising that this early endogenous component was not reliably sensitive to condition. It was important

to note, however, that the groups did not differ on the P200, indicating that there was no overall difference in EEG power between younger and older adults.

The P3a component, regarded to reflect stimulus classification (Kok, 2001), showed condition differences in younger adults but not older adults. When the younger adults were presented with a probe that matched one of the items in the target set held in working memory, there was a marked increase in the positive amplitude of the P3a in comparison to the negative baseline condition. Also, the salience of the familiar negative probes failed to elicit any "target-like" response in the P3a. Together this suggested that young adults had efficiently discriminated targets from all non-targets at this relatively early stage of processing.

The P3a waveforms of older adults were delayed relative to the younger adults, suggesting an age-related delay in matching probe to target set. Also, visual inspection of the waveforms for each condition suggested a more positive P3a response to response conflict trials and positive trials, in comparison to baseline. However, these differences failed to reach statistical significance. It seemed that older adults, although eventually making correct judgements about the identity of targets, failed to show target sensitivity in their P3a responses.

The P3b component, as conceptualized here, reflected attentional allocation to stimuli requiring further processing (Dywan et al, 2002). Younger adults, having distinguished target probes at the level of the P3a, also showed greater P3b response to positive targets in comparison to both the baseline and conflict conditions. Furthermore, the magnitude of the P3b was positively predicted by the P3a, such that younger participants who made a clear dissociation of targets from non-targets, at the

level of their P3a response, also produced a larger P3b response to targets relative to non-targets, suggesting that they were able to suppress the continued allocation of attention to the non-target stimuli. The P3b responses of older adults failed to show this level of specificity, mirroring the lack of differentiation seen in their P3a.

These findings partly conform to previous work done using source memory tasks. Dywan and colleagues (1998; 2001; 2002) found that younger adults appeared to make early discriminations of target identity and allocated attentional resources to further processing the positive targets while inhibiting further processing of non-targets. This target sensitivity likely relies on early selective attention processes in posterior cortices and *can* bias processing as early as 150-200 ms after stimulus presentation (Hillyard & Anllo-Vento, 1998). In the work of Dywan and colleagues (2002), the inclusion of salient lure probes seen 6 trials earlier did not result in a target-like P3b responses by younger adults. However, while older adults showed an elevated P3b to targets and suppressed P3b to simple non-targets, they showed target-like responses to the lure probes. This target-like response was thought to result from a failure to inhibit processing of non-target lures because of the salience created from the familiar lure overwhelming early selective attention processes in older adults. However, as these P3b responses were analyzed only on correct trials, as was done in the present study, it appeared that older adults were identifying the targets properly but at some later stage of processing. In the present data, older adults similarly failed to show the early sensitivity exhibited by younger adults but were able to produce the appropriate behavioural response.

This "early selection, late correction" model has been a subject of study in research on interference effects in memory by Jacoby and colleagues (Jacoby, Bishara, Hessels & Toth, 2005). Their behavioural work suggests that the presentation of a probe stimulus activates a set of representations. This initial activation likely relies on automatic processing in posterior brain regions. A later evaluation process, occurring in a more controlled manner and likely relying on frontal cortices, selects the appropriate response, based on the information automatically activated by the probe. When a lure is presented to younger and older adults, age differences occur at the initial selection stage but not at the later evaluation stage. Jacoby and colleagues (2005) suggest that one reason why older adults are more likely to act on the misinformation of the lure is because of a failure of inhibitory control in filtering the initially activated response set.

To better understand the process by which non-target stimuli are inhibited, several different interference manipulations were employed in the present study with the hopes of differentially engaging frontal brain regions signalling for and implementing cognitive control.

Electrophysiological Response to Interference. Research has suggested that a discrete fronto-central negativity occurring around 450 ms after the presentation of a target stimulus is modulated by interference from irrelevant but salient stimuli (Rebai, Bernard, & Lannou, 1997). Investigations in the Stroop task found that incongruent trials produced a greater N450 component than congruent trials and that this negativity, unique to the incongruent trials, therefore reflected the inhibition of competing word information (West & Alain, 1999). Research on age-related changes

in Stroop performance further indicated that older adults, having more difficulty overcoming the interference effects of competing colour words, produced an attenuated N450 component on their incongruent trials (West & Alain, 2000; West, 2004b).

In the present sample, the N450 showed considerable variability in both topography and latency in both younger and older adults. Through a series of exploratory analyses, it was found that a composite of frontal sites, as opposed to a traditional single site analysis, revealed significant differences between both the familiar and response conflict conditions in comparison to the baseline negative condition in the younger group. The highly familiar condition failed to show a significant increase in the amplitude of the N450 relative to the familiar condition with only one repetition.

The older adults, although not showing marked decreases in behavioural performance, were expected to show an attenuated N450 component in comparison to the younger group (West & Allain, 2000; West, 2004b). In fact, it appeared that the older group, as a whole, failed to show any evidence of an N450. However, inspection of the neural responses of individual older adults indicated that many of the senior participants were producing a frontal negativity indicative of the N450. It seemed, though, that the individual variability in the scalp locations of their N450 responses and a diffuse frontal positivity occurring throughout the 400-500 ms time window of several individuals obscured the negativity in the group average. Exploratory analyses revealed that the topographical variability in the N450 component was, in fact, partially determined by task condition, such that familiar and

response conflict conditions showed lower variability than the baseline condition. It could be that increasing condition difficulty resulted in a focusing of neural response. However, the result should be interpreted with caution and a replication should be done to increase confidence that this is a reliable finding.

In sum, the older adults failed to show a differential negativity to interference trials while younger adults showed that their N450 responses were sensitive to the interference created by the familiarity-based and response-based conflict trials. However, the present data did not provide a reliable dissociation between the N450 components of the familiar and response conflict conditions in the young adults. A main finding of Nelson and colleagues (2003) was the dissociation of activity between the IFC for familiar trials and additional activity in ACC for response conflict trials. Considering that the IFC and ACC are both thought to contribute to the N450 (Markela-Lerence et al, 2004) it was believed that the N450 may be significantly larger in the response conflict condition than the familiar condition. This was not the case in the current data. However, there has been a growing debate as to whether the ACC is as uniquely associated with cognitive control processes, such as in response-conflict resolution, as originally thought (e.g., Fellows & Farah, 2005).

Recent work by West and colleagues (2004a) has shown that an N450 response is similarly produced when the conflicting colour word, as in the Stroop task, is not a member of the possible response set (i.e., the word "green" is present but green is not one of the ink colours used in the task). If there is no conflict in the response set, then there should be no evidence of interference in the ERP waveforms because there was no prepotent response mapping to overcome. West and colleagues (2004a) used

source analysis techniques to investigate the neural generators of the N450 in the response conflict and non-response conflict trials. Both trial types produced a similar N450 with neural generators in inferior frontal cortex and anterior cingulate cortex. Their results supported the notion that the N450 was not specific to conflict-based interference at the response selection stage, but reflected a more general inhibitory process that occurs when a response is withheld irrespective of the context in which inhibition occurs.

In order to better understand the potential role of inferior frontal cortex and anterior cingulate cortex in the present investigation, preliminary dipole source analyses were done on the N450 components produced by the younger adults. As older adults did not produce a clear N450 and showed diffuse positive activity in the N450 time window, it was beyond scope of the present preliminary source analysis to model dipoles for this group.

Dipole models of the N450 familiar and response conflict condition for younger adults suggested symmetrical primary generators in inferior frontal cortex and a generator in anterior cingulate cortex. These sources are similar to the neural generators found for the N450 in the context of the Stroop paradigm (Markela-Lerenc et al., 2004). The generator in the anterior cingulate accounted for a greater portion of activity in the response conflict condition than the familiar condition, suggesting a greater degree of ACC activation in the response conflict than for the familiar trials. However, this shift in the influence of the ACC was not accompanied by reliable condition-related difference in the N450 component at the scalp. Thus, the present findings appear to be in line with the findings of the West and colleagues (2004a) in

that they suggest a general response inhibition function and do not provide support for the clear dissociation between IFC and ACC suggested by Nelson and colleagues (2003).

An additional question to be addressed in this study involved the time course of inferior frontal cortex and anterior cingulate contributions to the N450. It was found that peak activity of the IFC generator occurred approximately 30 ms prior to the peak activity of the ACC generator. These findings are also in line with the results of Markela-Lerenc and colleagues (2004). Using the Stroop paradigm, they showed that prefrontal contribution to the N450 preceded activity in the ACC. Taken together, the results of Markela-Lerenc and colleagues (2004) and the present results suggest that prefrontal cortex may signal the need for increased cognitive control leading to the recruitment of the ACC.

Neural Responses of Older Adults: Deterioration versus Compensation. An original expectation for the current study was that, in comparison to younger adults, older adults would show marked increases in error rates and response times as the interference conditions became more difficult. This hypothesis was based on research supporting the lesion model of cognitive aging (Reuter-Lorenz, 2002). This model focuses on the behavioural losses associated with aging, such as reduced processing speed, increased forgetting, greater error rates, and poorer perceptual processing. In turn, these behavioural changes are associated with the decline in functioning of specific brain areas, especially the frontal lobes (West, 1996). However, close inspection of such findings reveal that the true extent of such losses and their consequences are not as severe as once thought (e.g., Band, Riddernkhof &

Segalowitz, 2002). Furthermore, actual changes to neurons in specific cortices do not necessary entail a dramatic loss of functioning (Della Salla, Gray, Spinnler & Trivelli, 1998). Understanding that age-related changes to brain function and structure are actually quite specific has tempered the view that cognitive aging should be described solely as a deficit-laden trajectory. Newer models of cognitive aging are incorporating compensation and reorganization processes into explaining the *differences*, as opposed to *deficits*, seen in the aging brain.

One of the most important findings to come out of this new view is that, in tasks where behavioural performance appears to be comparable between age groups, the pattern of neural responses in older adults is quite different from that of younger adults. This suggests that the older adults are relying on different or additional brain areas to successfully complete a given task. The present study is an example of such a finding. The ERPs of older adults appeared quite distinct from younger adults, especially with regards to a diffuse frontal positivity occurring in tandem with the N450. Despite this difference in brain response, older adults showed nearly equal interference effects in their behavioural performance in comparison to younger adults.

Recent imaging work on age-related changes in cognitive functioning have shown that older adults often show activity in brain areas not recruited by younger adults when completing cognitive tasks of varying difficulty and task demands (Reuter-Lorenz, 2002). Early work on compensation theories in cognitive neuroscience have suggested that additional activity in the brains of older adults can index the recruitment of processing resources needed to efficiently complete a given task (Grady, Maisog, Horwitz, Ungerleider, et al., 1994). Grady and colleagues

(1994) used PET measures of neural responses in younger and older adults as participants matched stimuli based on identity (i.e., face stimuli) or by stimulus location. Much like the present study, older adults showed accuracy rates on par with younger adults. Imaging results indicated that younger adults, as expected, showed discrete temporal cortex activity for faces and parietal cortex activity for location. Older adults, in contrast, showed activity in both these regions for each separate stimulus set. The lesion model of cognitive aging would suggest that older adults were not efficiently switching their processing sets between the tasks. However, as this activity did not appear to hamper the older adults' accuracies, a more interesting explanation would be that older adults benefited from this dual activation. More recent research (Reuter-Lorenz, 2002) has made similar assertions and suggests that this compensatory profile of altered neural responses in older adults would be possible to the extent that the individual's brain can reorganize functions through plasticity.

Other lines of research have validated compensation theories by showing that age-related over-activation of specific brain regions is correlated with improved performance (McIntosh, Sekuler, Panpeci, Rajah, Grady et al., 1999; Reuter-Lorenz et al, 2002; Rypma & D'Esposito, 2001). The brain region most associated with compensatory activity has been suggested to be prefrontal cortex (Cabeza, Daselaar, Dolcos, Prince, Budd & Nyberg, 2004). Additionally, Cabeza and colleagues (2004) suggest that compensatory activity in PFC often takes the form of bilateral activation, as opposed to the asymmetric activation in younger adults. This Hemispheric Asymmetry Reduction in Older Adults (or HAROLD model) has been supported by

imaging and electrophysiological findings from a variety of tasks (see Cabeza, et al., 2002 for a review).

In the present study, many of the older adults produced slow-going positive amplitudes over bilateral frontal cortices either accompanying or superseding their N450 activity. Although the older adults' activity in the 400-500 ms window of the N450 did not differentiate among conditions, it did consistently correlate with the amplitude of the P3a wave. It is possible that compensatory prefrontal activity, occurring as bilateral positive activity during the latency window associated with the N450, could be the source of the variance supporting the "N450" correlation with the P3a. Unfortunately, as the N450 and these potentially compensatory positivities are of opposite polarity, their individual activities may cancel each other out to some extent, making it more difficult to observe the unique contributions of each individual process. Also, because of this cancelling effect, it is very difficult to discriminate older adults who are showing both N450 and prefrontal positivities from other older adults producing little evidence of either effect, as the end result of either response profile is similar. It is tantalizing to view the older adults neural responses as adaptive. However, as there were no direct relationships between performance and ERP measures, this notion is currently confined to speculation. In conclusion, it appeared that this differential neural response of older adults did not dramatically hinder their performance in comparison to younger adults. However, further investigation will be necessary to reliably identify any *beneficial*, as opposed to inconsequential, effects of age-related changes in neural response to interference in the current paradigm.

Limitations and Future Directions. Several issues arose in the present study in the form of methodological limitations. First, as the Sternberg task used only 20 letters, there was a continuous recycling of target and probe stimuli aside from the strategic repetition of stimuli for the respective task manipulations. For example, the lower-case consonant "n" would be expected to be seen a total of 70 times by the completion of the experiment, with only a small fraction of these relating to the experimental manipulations. The repetition of the same 20 stimuli in non-manipulated trials may have resulted in a context-based interference effect in every trial, including the negative baseline and positive conditions. As was seen in Figures 6a & 6b, both the positive and negative trials appeared to elicit an N450-like activity even though there was no interference manipulation in either of these conditions. Therefore, a non-specific neural response to this ubiquitous stimulus familiarity could have created a general conflict-related ERP in every trial, which could resemble an N450. Fortunately, as trials are presented pseudo-randomly, it should not have confounded any particular condition. The non-specific familiarity effect should be a constant and be additive to the effects of the task manipulation, allowing for any underlying differences to be preserved. Unfortunately, this non-specific familiarity effect may have added variance to the N450 components and decreased the power of the present analyses to find difference between conditions as well as reducing the strength of correlations between the N450 and other behavioural and ERP measures.

Investigating the nature of this non-specific N450 activity is an issue in itself. It would be interesting to test the ideas presented here by running a new sample of participants on the present task and testing an additional task with the same

interference conditions but employing a large body of stimuli, such as simple words, in which stimulus repetitions are confined to the task manipulations. If the condition specific N450 was found in both tasks, but the non-specific N450 was only found in the Sternberg task using letters, it would demonstrate the power of long-term stimulus repetitions as well as demonstrating a method for producing a cleaner measure of the N450.

Another issue requiring further investigation regards the suggestion that the positivity seen in the older adults' N450 time window may be indicative of compensatory activity. Reliably measuring this activity can prove challenging as it coincides with other discrete brain responses, such as the N450 in the present paradigm. Some researchers have identified tasks that create a context in which compensatory activity can be separated from other event-related activity (e.g., Cabeza et al., 2002). However a more useful approach may be offered by new computational techniques for separating the correlated signals in EEG data. Such signal processing techniques may provide an avenue for the separation of raw EEG data into separate waveforms representing multiple discrete activities. Independent component analysis (ICA, Delorme & Makeig, 2004; for an example of applications see Debener, Makeig, Delorme & Engel, 2005) is one such tool that could separate the N450 activity and the co-occurring positivity in the older adults, allowing for positive activity to be represented as its own measure for use in indexing performance or correlating to other behavioural or physiological measures.

Finally, it would be interesting to further investigate the parameters of the N450 as it relates to the efficiency of other functions of the central executive. For example,

is a participant's capacity to produce the interference-related N450 altered systematically by working memory load (Lavie, Hirst, de Fockert & Viding, 2004). Also it will be important to continue the investigation of the neural generators of the N450 in order to identify how task demands determine the activation of inferior prefrontal and anterior cingulate cortex.

References

Aycicegi, A., Dinn, W. M., Harris, C. L. & Erkmen, H. (2003). Neuropsychological Function in Obsessive-Compulsive Disorder: Effects of Comorbid Conditions on Task Performance. *European Psychiatry, 18*, 241-248.

Anderson, J. R., Reder, L. M. & Lebiere, C. (1996). Working Memory: Activation Limits on Retrieval. *Cognitive Psychology*, 30, 221-256.

Anderson, M, C. & Spellman, B, A. (1995). On the status of inhibitory mechanisms in Cognition: Memory retrieval as a model case. *Psychological Review*, 102, 68-100.

Baddeley, A. D., Emslie, H. & Nimmo-Smith, I. (1992). *The speed and capactivy of language processing (SCOLP) test.* Thames Valley Test Company, Bury St. Edmunds.

Band, G. P. H., Ridderinkhof, K. R. & Segalowitz, S. (2002). Explaining neurocognitive aging: Is one factor enough? *Brain & Cognition*. 49, 259-267.

BESA, version 5.1, Megis Corporation, Munich. 2004.

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S. & Cohen, J. D. (2001). Conflict Monitoring and Cognitive Control. *Psychological Review*, 108, 624-652.

Braver, T. S., Barch, D. M., Keys, B. A., Cameron, S., Cohen, J. D. et al., (2001). Context Processing in Older Adults: Evidence for a Theory Relating Cognitive Control to Neurobiology in Healthy Aging. *Journal of Experimental Psychology: General*, 130, 746-763.

Braver, T. S. & Barch, D. M. (2002). A Theory of Cogntive Control, Aging, Cognition, and Neuromodulation. *Neuroscience & Biobehavioural Reviews*, 26(7), 809-817.

Braver, T. S., Cohen, J. D. & Barch, D. M. (2002). The Role of Prefrontal Cortex in Normal and Disordered Cognitive Control: A Cognitive Neuroscience Perspective. In Stuss, D. T. & Knight, R. T. (Eds.). *Principles of Frontal Lobe Function* (428-447). London, Oxford Press.

Bunce, D. (2003). Cognitive support at encoding attenuates age differences in recollective experience among adults of lower frontal lobe function. *Neuropsychology*, 17, 353-361.

Bunge, S.A., Ochsner, K.N., Desmond, J.E. Glover, G.H. & Gabrieli, J.D.E. (2001). Prefrontal regions involved in keeping formation in and out of mind. *Brain, 124,* 2074-2086.

Cabeza, R. (2001). Cognitive Neuroscience of Aging: Contributions of Functional Neuroimaging. *Scandinavian Journal of Psychology*, 42, 277-286.

Cabeza, R., Daselaar, S. M., Dolcos, F., Prince, E. S., Budde, M. & Nyberg, L. (2004). Task-independent and task-specific age effects on brain activity during working memory, visual attention and episodic retrieval. *Cerebral Cortex,* 14, 364-375.

Cohen, J. & Servan-Schreiber, D. (1992). Context, cortex and dopamine: A connectionist approach to behaviour and biology in schizophrenia. *Psychological Review, 99*, 45-77.

Connelly, S.L., Hasher, L. & Zack, R.T. (1991). Age and reading: The impact of distraction. *Psychology and Aging*, *6*, 533-541.

Craik, F. & Salthouse, T. A. (Eds). (2000). *The Handbook of Aging and Cognition (2nd Ed.).* Mahwah, NJ, US: Lawrence Erlbaum Associates.

Crowley, K. E. & Colrain, I. M. (2004). A review of the ecidence for P2 being and independent component process: Age, sleep and modality. *Clinical Neuropsychology*, 115, 732-744.

Crum, R. M., Anthony, J. C., Bassett, S. S. & Folstein, M. F. (1993). Population-based norms for the Mini-Mental State Examination by age and educational level. *Journal of the American Medical Association*. 269, 2386-2391

Debener, S., Makeig, S., Delorme, A., Engel, A.K. (2005) What is novel in the novelty oddball paradigm? Functional significance of the novelty P3 event-related potential as revealed by independent component analysis. *Cognitive Brain Research*, 22(3), 309-321.

D'Esposito, M., Postle, B.R., Ballard, D. & Lease, J. (1999). Maintenance versus manipulation of information held in working memory: an event-related fMRI study. *Brain and Cognition, 41*, 66-86.

Delorme, A., Makeig, S. (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9-21.

de Forket, J.W., Rees, G., Frith, C.D. & Lavie, N. (2001). The role of working memory in visual selective attention. *Science, 291*, 1803-1806.

Della Salla, S., Gray, C., Spinnler, H. & Trivelli, C. (1998). Frontal lobe functioning in man: The riddle revisited. *Archives of Clinical Neuropsychology*, 13, 663-682

Dimitrov, M., Nakic, M., Elpern-Waxman, J., Granetz, J., O'Grady, J., Phipps, M., Milne, E., Logan, G. D., Hasher, L. & Grafman, J. (2003). Inhibitory attentional control in patients with frontal lobe damage. *Brain and Cognition, 52*, 258-270.

Demasio, A.R. (1998). The somatic marker hypothesis and the possible functions of the prefrontal cortex. In: Roberts, A.C., Robbins, T.W. & Weiskrantz, L. *The prefrontal cortex: Executive and cognitive functions* (page 37-50check).

Dywan, J., Segalowitz, S. J. & Webster, L. (1998). Source Monitoring: ERP Evidence for Greater Reactivity to Non-Target Information in Older Adults. *Brain & Cognition*, 36(3), 390-430.

Dywan, J., Segalowitz, S. J., Webster, L., Hendry, K. & Harding, J. (2001). ERP Evidence for Age-Related Differences in Attentional Allocation During a Source Monitoring Task. *Developmental Neuropsychology*, 19(1), 99-120.

Dywan, J., Segalowitz, S. J. & Arsenault, A. (2002). Electrophysiological Response During Source Memory Decisions in Older and Younger Adults. *Brain & Cognition*, 49(3), 322-340.

Dywan, J. & Murphy, W. (1996). Aging and Inhibitory Control in Text Comprehension. *Psychology & Aging*, 11(12), 199-206.

Ellwanger, J., Geyer, M. A., & Braff, L. D. (2003). The Relationship of Age to Prepulse Inhibition and Habituation of the Acoustic Startle Response. *Biological Psychology, 62*, 175-195.

Fellows, L.K. and Farah, M.J. (2005). Is anterior cingulate cortex necessary for cognitive control? *Brain,* 128, 788-796.

Folstein, M.F., Folstein, S.E., & McHugh, P.R. (1975). "Mini-Mental State": A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research,* 12, 189-198.

Frishkoff, G. A., Tucker, D. M., Davey, C. & Scherg, M. (2004). Separation of anterior and posterior brain sources of event-related potentials in semantic comprehension. *Cognitive Brain Research*. 20. 329-254.

Giraud, A. L., Kell, C., Theirfelder, C., Sterzer, P., Russ, M. O., Preibisch, C. & Kleinschmidt, A. (2004). Contributions of Sensory Input, Auditory Search and Verbal Comprehension to Cortical Activity During Speech Processing. *Cerebral Cortex*, 14(3), 247-255.

Gold, D., Andres, D., Arbuckle, T. & Schwartzman, A. (1988). Measurement and correlates of verbosity in elderly people. *Journal of Gerontology*, 43, 27-33.

Gerard, L., Zacks, R. T., Hasher, L. & Radvansky, G. A. (1991). Age Deficits in Retrieval: The Fan Effect. *Journals of Gereontology*, 46, 131-136.

Grady, C. (2002). Age-related differences in face processing: A meta-analysis of three functional neuroimaging experiments. *Canadian Journal of Experimental Psychology*, 56, 208-220.

Grady, C. L., Maisog, J. M., Horwitz, B. & Ungerleider, L. G., et al. (1994). Age-related changes in cortical blodd flow activation during visual processing of faces and location. *Journal of Neuroscience.* 14, 1450-1262.

Gutchess, A.H., Welsh, R. C., Hedden, T., Bangert, A., Minear, M., et al., Aging and the neural correlates of successful picture encoding: Frontal activations compensate for decreased medial-temporal activity. *Journal of Cognitive Neuroscience*, 17, 84-96.

Hadjikhani, H. & de Gelder, B. (2002). Neural Basis of Propopagnosia: An fMRI study. *Human Brain Mapping,* 16 , 176-182.

Hamm, V, P., & Hasher, L. (1992). Age and the availability of interference. *Psychology and Aging*, 7, 1-10.

Hartman, M., & Hasher, L. (1991). Aging and suppression: Memory for previously relevant information. *Psychology and Aging*, 6, 587-594.

Hartley, A., A. (1992). Attention. In F.I.M. Creaik & Salthouse (Eds.). *The handbook of aging and cognition* (3-49). Hillsdale, NJ: Erlbaum.

Hasher, L., Chung, C., May, C., & Foong, N. (2002). Age, Time of Testing, and Proactive Interference. *Canadian Journal of Experimental Psychology*, 56, 200-207.

Hasher, L. & Zacks, R, T. (1988) Working Memory, comprehension and aging: A review and a new view. In G.H. Bower (Ed.), *The psychology of learning and motivation* (22, 193-225). New York, Academic Press.

Hasher, L, Zacks, R. T., & May S. P. (1999). Inhibitory Control, Circadian Arousal, and Age. In Gopher, D. & Koriat, A. (EDs.). *Attention and performance XVII: Cognitive regulation of performance: Interaction of theory and application.* (653-675). Cambridge, The MIT Press.

Hasher, L., Zacks, R. T. & Rahhal, T. A. (1999). Timing, Instructions, and Inhibitory Control: Some Missing Factors in the Age and Memory Debate. *Gerontology*, 45, 355-357.

Hazeltine, E., Poldrack, R. & Gavrieli, J.D.E. (2000). *Journal of Cognitive Neuroscience, 12 (supp. 2),* 118-29.

Hazeltine, E., Bunger, S. A., Scanlon, M. D. & Gabrieli, J. D. E. (2003). Material-dependent and material-independent selection processes in the frontal and parietal lobes: An event-related fMRI investigation of response competition. *Neuropsychologia*, 41, 1208-1217.

Herron, J. E., Quayle, A. H. & Rugg, M. D. (2003). Probability Effects on Event-Related Potential Correlates of Recognition Memory. *Cognitive Brain Research*, 16, 66-73.

Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences*, 95, 781–787.

Houghton, G. & Tipper, S.P. (1994). A model of inhibitory mechanisms in selective attention. In Deganbach, D. & Thomas, C.H. (Eds.), *Inhibitory Processes in Attention, Memory, and Language* (53-112). Toronto, Academic Press.

Jacoby, L. L., Bishara, A. J., Hessels, S. & Toth, J. P. (2005). Aging, Subjective Experience, and Cognitive Control: Dramatic False Remembering by Older Adults. *Journal of Experimental Psychology: General.* 134, 131-148.

Jonides, J., Marshuetz, C., Smith, E., Reuter-Lorenz, P. A., Koeppe, R. A. & Hartley, A. (2000). Age Differences in Behaviour and PET Activation Reveal Differences in Interference Resolution in Verbal Working Memory. *Journal of Cognitive Neuroscience,* 12, 188-196.

Johnson, R., Pfefferbaum, A. & Kopell B.S. (1985) P300 and long-term memory: latency predicts recognition performance. *Psychophysiology.* 22, 497-507.

Kane, M. J., Hasher, L., Stoltzfus, E. R. & Zacks, R. T. (1994). Inhibitory Attentional Mechanism and Aging. *Psychology & Aging*, 9, 103-112.

Kiefer M, Marzinzik F, Weisbrod M, Scherg M, Spitzer M. (1998). The time course of brain activations during response inhibition: evidence from event-related potentials in a go/no go task. *NeuroReport*, 9, 765-70.

Kok, A., 2001. On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology,* 38, 557–577.

Konishi, S., Nakajima, K., Uchida, I., Kikyo, H., Kameyama, M., Miyashita, Y. (1999). Common inhibitory mechanism in human inferior prefrontal cortex revealed by event-related fMRI. *Brain,* 122, 981-991.

Lavie, N., Hirst, A., De Fockert, J.W., & Viding, E. (2004). Load theory of selective attention and cognitive control. *Journal of Experimental Psychology: General*, 133, 339-354.

Liotti, M., Woldorff, M. G., Perez, R. III. & Mayberg, H. S. (2000). An ERP Study of the Temporal Course of the Stroop Colour-Word Interference Effect. *Neuropsychologia*, 38, 701-711.

Lowe, C. & Rabbitt, P.M.A. (1997). Cognitive models of ageing an frontal lobe deficits. In Rabbitt, P.M.A. (Ed), *Methodology of frontal and executive function* (39-59). Hove, E. Sussex, England: Psychology press.

Lustig, C., May, C. & Hasher, L. (2001). Working Memory Span and the Role of Proactive Interference. *Journal of Experimental Psychology: General.* 130, 199-207.

Madden, D. J. (1986). Adult Age Differences in the Attentional Capacity Demands of Visual Search. *Cognitive Development*, 1, 335-363.

Madden, D. J. (1987). Aging, Attention, and the use of Meaning During Visual Search. *Cognitive Development*, 2, 201-216.

MacLeod, C. M., Dodd, M. D., Sheard, E. D., Wilson, D. E., & Bibi, U. (2003). In opposition to inhibition. In B. H. Ross (Ed.), *The Psychology of Learning and Motivation*, Vol. 43 (pp. 163-214). San Diego, CA: Academic Press.

Markela-Lerenc, J., Ille, N., Kaiser, S., Fiedler, P., Mundt, C. & Weisbrod, M. (2004). Prefrontal-Cingulate Activation During Executive Control: Which Comes First? *Cognitive Brain Research*, 18, 278-287.

Mason, D. J., Humphreys, G. W. & Kent, L. S. (2003). Exploring Selective Attention in ADHD: Visual Search Through Space and Time. *Journal of Child Psychology and Psychiatry,* 44, 1158-1176.

McIntosh, A. R., Sekuler, A.B., Panpeci, C., Rajah, M. N., Grady, C. L., Sekuler, R. & Bennet, P. J. (1999). *Currently Biology.* 9, 1275-1278.

Mecklinger, A., Weber, K., Gunter, T. C. & Engle, R. W. (2003). Dissociable Brain Mechanisms for Inhibitory Control: Effects of Interference Content and Working Memory Capacity. *Cognitive Brain Research.* 18, 26-38.

Milham, M. P., Banich, M. T., Webb, A., Barad, V., Cohen, N. J., Wszalek, T. & Kramar, A. F. (2001). The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Cognitive Brain Research,* 12, 467-473.

Miller, E.K. & Cohen, J.D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience,* 24, 167-202.

Narayanan, N. S., Prabhakaran, V., Bunge, S. A., Christoff, K., Fine, M. & Gabrieli, J. D. E. (2005). The Role of the Prefrontal Cortex in the Maintenance of Verbal Working Memory: An Event-Related fMRI Analysis. *Neuropsychology,* 19. 223-232.

Nelson, K., Reuter-Lorenz, P. A., Sylvester, C.Y. C., Jonides, J. & Smith, E. (2003). Dissociable Neural Mechanisms Underlying Response-Based and Familiarity-Based Conflict in Working Memory. *PNAS,* 100, 11171-11175.

Oberauer, K. (2001). Removing irrelevant information from working memory. An age-comparative study with the modified Sternberg task. *Journal of Experimental Psycholgy: Learning, Memory, and Cognition,* 27, 948-957.

Phillips, L., MacPherson, S. & Della Sala, S. (2002). Age, cognition, and emotion: The role of anatomical segregation in the frontal lobes. In Grafman, J. (Ed.), *Handbook of neuropsychology (2nd ed.): Vol 7, The frontal lobes* (73-97). Amsterdam: Elsevier Science B.V.

Quintana, J. & Fuster, J. M. (1999). From Perception to Action: Temporal Integrative Functions of Prefrontal and Parietal Neurons. *Cerebral Cortex*, 9, 213-221.

Rabbitt, P. (1965). An age-decrement in the ability to ignore irrelevant information. *Journal of Gerentology*, 20, 233-238.

Rainer, G., Assad, W. F. & Miller, E. K. (1998). Selective Representations of Relevant Information by Neurons in the Primate Prefrontal Cortex. *Nature*, 393, 577-579.

Raz, N. (2000). Aging of the Brain and its Impact on Cogntive Performance: Integration of Structual and Functional Findings. In Craik, F. I. M. & Salthouse, T.A. (Eds). *The handbook of aging and cognition* (2nd Ed.) Mahwah, NJ, US: Lawrence Erlbaum Associates.

Rebai, M., Bernard, C. & Lannou, J. (1997). The Stroop test evokes a negative brain potential, the N400. *International Journal of Neuroscience*, 91, 85–94

Rebai, M., Christian, B. & Lanou, J. (1997). The Stroop's Test Evokes a Negative Brain Potential, the N400. *International Journal of Neuroscience*, 91, 85-94.

Reitan, R.M., 1979. Trail Making Test (TMT). Hogrefe-Verlag, Gottingen, Germany.

Reuter-Lorenz, P. A. (2002). New visions of the aging mind and brain. *Trends in Cognitive Sciences*, 6, 394-400.

Ridderinkoff, K. R., van den Wildenberg, W. P. M., Segalowitz, S. J. & Carter, C. S. (2004). Neurocognitive mechanisms of cognitive control: The role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning. *Brain & Cognition*, 56, 129-140.

Rypma, B. & D'Esposito, M. (2001). Age-related changed in brain-behaviour relationships: evidence from event-related functional MRI studies. *European Journal of Cognitive Psychology*, 13, 235-256.

Salthouse, T. A. (1988). The role of processing resources in cognitive aging. In M.L. Howe & C.J. Brainard (Eds.), *Cognitive development in adulthood* (185-239). New York: Springer-Verlag.

Salthouse, T. A. & Meinz, E. (1995). Aging, Inhibition, Working Memory, and Speed. *Journal of Gerontology,* 50, 297-305.

Salthouse, T. A. (1996). The Processing-Speed Theory of Adult Age Differences in Cognition. *Psychological Review,* 103, 403-428.

Salthouse, T.A. & Hedden, T. (2002). Interpreting reaction time measures in between-group comparisons. Journal of Clinical and Experimental *Neuropsychology*, 24, 858-872.

Sawaguchi, T., Matsumura, M. & Kubota, K. Effects of Dopamine Antagonists on Neuronal Activity Related to a Delayed Response Task in Monkey Prefrontal Cortex. *Journal of Neurophysiology*, 63, 1201-1412.

Stroop, J. R. (1935). Studies of Interference in Serial Verbal Reactions. Journal of Experimental Psychology, 18, 643-661.

Thompson-Schill, S.L., D'Esposito, M., Aguirre, G.K. & Farah, G.K. (1997). Role of the left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc Natl Acad Sci USA,* 94, 14792-14797.

van Boxtel, G.J.M. (2004). The use of the subtraction technique in the psychophysiology of response inhibition and conflict. In M. Ullsperger & M. Falkenstein (Eds.), *Errors, Conflicts, and the Brain. Current Opinions on Performance Monitoring.* (pp. 219-225). Leipzig: Max Planck Institute of Cognitive Neuroscience.

van Veen, V., Holroyd, C. B., Cohen, J. D., Stenger, A. V. & Carter, C. S. (2004). Errors Without Conflict: Implications for Performance Monitoring Theories of Anterior Cingulate Cortex. *Brain & Cognition*, 56, 267-276.

William, G. V. & Goldman-Rakic, P. S. (1995). Modulation of Memory Fields by Dopamine D1 Receptros in Prefrontal Cortex. *Nature*, 376, 572-575.

West, R.J. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin,* 120, 272-292.

West, R. & Alain, C. (1999). Event-related neural activity associated with the Stroop task. *Cognitive Brain Research*, 8, 157-164.

West, R. & Alain, C. (2000). Age-related decline in inhibitory control contributes to the increased Stroop effect observed in older adults. *Psychophysiology*, 37, 179-189.

West, R. J., Bowry, R. & McConville, C. (2004a). Sesnsitivity of Medial Frontal Cortex to Response and Non-Response Conflict. *Psychophysiology*, 41, 739-748.

West, R. J. (2004b). The Effects of Aging on Controlled Attention and Conflict Processing in the Stroop Task. *Journal of Cognitive Neuroscience*, 16(1), 103-113.

Yeung, N., Botvinick, M. M. & Cohen, J. D. (2004) The Neural Basis of Error Detection: Conflict Monitoring and the Error-Related Negativity. *Psychological Review*, 111(4), 931-959.

Zhang, X., Wang, Y., Li, S. & Wang, L. (2003). Event-related potential N270, a negative component to identification of conflicting information following memory retrieval. Clinical *Neuropshysiology*, 114, 2461-2468.

Zigmund, A.S. and Snaith, RP. (1983) The Hospital Anxiety and Depression Scale. *Acta Psychiatrica Scandinavia*, 67, 361-370.

Footnotes

1. Exerting *restraint* over incorrect prepotent response tendencies is also mentioned in their model but does not take a central role in their theory and is not the focus of empirical work supporting the model.

2. The original terminology used by Nelson et al., (2003) was interference due to *familiarity*. However, their methodology is in line with the term context-based interference, and so that term is used for the sake of consistency.

3. Since the response conflict trial has two exposures to a critical probe (as both a target and then a probe on previous trial) the highly familiar trial (two presentations as targets) should be a better comparison than the simple familiar trial (one presentation as a target).

4. As the Sternberg task used only 20 letters, there was a continuous recycling of target and probe stimuli. For example, the lower-case consonant "n" would be expected to be seen a total of 70 times by the completion of the experiment, with only a small fraction of these relating to the experimental manipulations. The repetition of the same 20 stimuli in non-manipulated trials may have resulted in a context-based interference effect in every trial, including the negative baseline positive condition. As seen in Figures 7a and 7b, both the positive and negative trials appeared to elicit an N450-like activity even though there was no interference manipulation in either of these conditions. Therefore, a non-specific neural response to this ubiquitous stimulus familiarity could have created a general conflict-related ERP in every trial, which could resemble an N450.

5. This wide sampling range was required as the latencies of the P3a were quite variable, particularly in the older group.

6. This trend was mainly due to the difference between the familiar and response conflict condition. The a-priori t-test between the older adults' baseline and positive conditions was non-significant $t(17) = .13$, *n.s.*

7. Although the P3b appeared to begin near 350 ms, beginning the sampling at this time point would have included activity associated with the P3a.

8. Alternative analyses were done with the positive condition included and resulted in no changes to the null hypothesis decisions, based on respective *F*-values.

9. Although the variance of the distribution of scores for younger and older adults are similar the magnitude of scores on many of the measures were quite different between groups. For example, younger adults, as a group, would show higher accuracy and greater amplitudes for ERP components from targetness and conflict processing while older adults would show both lower accuracy and smaller amplitudes in their ERPs. Conducting correlations using both younger and older

adults combined created a confound in the analysis such that the two groups tended to cluster at opposite corners of a given scatterplot. Although the individual group would show little evidence of a relationship, the correlation across both groups would produce a significant correlation. For this reason, the relationships between measures were done on each group separately. This did introduce a critical limitation though, as the respective power of the analyses in each group was greatly reduced due to decreases in N values.

10. In order to exclude error variance associated with individual differences in ERP responses, the measures used for the purpose of all correlations were constructed by removing the covariance shared by the baseline from the other condition of each individual. This technique is similar to a difference wave but avoids some of the confounds involved in creating simple difference waves in EEG data (see van Boxtel, 2004).

11. Dipole modeling was tested by subtracting the positive or negative condition from the conflict conditions and gave generally similar results. However, these models resulted in larger residual variance values than the models done on the intact original waveforms. Therefore, the dipole models of the unchanged waveforms were reported here.

Tables and Figures

Table 1.
Demographic Information and Results of Paper and Pencil Questionnaires for Younger and Older Adults.

	Age (yrs)	*Ed. (yrs)*	*SCOLP*	*HADS Anx.*	*HADS Dep.*	*TrailsA (sec.)*	*TrailsB (sec.)*	*MMSE*
Young	20 (1.9)	14.4 (1.0)	46.6 (4.6)	7.1 (3.6)	2.4 (1.8)	28.9 (11.4)	53.6 (20.1)	- -
Old	74.3 (7.3)	14.8 (2.3)	52.1 (4.7)	4.6 (2.2)	3.0 (2.9)	47.4 (14.2)	110.8 (37.9)	28.6 (1.2)

Table 2.

Mean Percentage of Correct Responses and Standard Deviations for each Condition of the Sternberg Task.

	Task Condition				
	Positive	*Baseline*	*Familiar*	*Highly Familiar*	*Response Conflict*
Group					
Young	.91 (.06)	.98 (.02)	.98 (.03)	.97 (.04)	.92 (.05)
Old	.89 (.09)	.97 (.03)	.96 (.04)	.92 (.05)	.91 (.04)
Total	.90	.98	.97	.94	.91

Table 3.
Mean Response Times and Standard Deviations in Milliseconds to Correct Trials in each Condition of the Sternberg Task and Group Difference Score (Old minus Young).

	Task Condition				
	Positive	*Baseline*	*Familiar*	*Highly Familiar*	*Response Conflict*
Group					
Young	762 (104)	812 (143)	850 (156)	889 (154)	922 (186)
Old	968 (180)	1038 (179)	1085 (199)	1162 (220)	1177 (234)
Old –Young	206	226	235	273	255

Note. Response Times were trimmed by removing trials that were ± 3 standard deviations beyond the individual participant's mean.

Table 4.
Mean P200 Amplitudes for Each Condition and Age Group at Midline Sites.

		Task Condition				
		Positive	*Baseline*	*Familiar*	*Highly Familiar*	*Response Conflict*
Group	*Site*					
Younger	FPz30	3.28	3.50	2.83	2.89	2.91
	Fz15	2.44	2.97	2.28	2.51	2.40
	Cz257	1.98	2.49	2.34	2.61	1.96
	Pz100	1.54	2.18	1.76	2.15	1.41
	Oz120	1.84	1.94	0.94	1.25	1.59
	M	2.22	2.62	2.03	2.28	2.05
Older	FPz30	2.18	2.98	2.53	2.76	2.79
	Fz15	2.52	2.89	2.80	2.89	3.39
	Cz257	2.43	2.51	2.48	2.75	3.16
	Pz100	2.32	2.18	2.01	2.43	2.79
	Oz120	1.48	1.94	1.23	1.32	2.29
	M	2.19	2.50	2.21	2.43	2.88

Table 5.

Mean P3a Amplitudes for Each Condition and Age Group at Midline Sites.

		Task Condition				
		Positive	*Baseline*	*Familiar*	*Highly Familiar*	*Response Conflict*
Group	*Site*					
Young	FPz30	3.47	2.40	2.05	2.58	2.14
	Fz15	0.86	-0.20	-0.27	-0.11	0.06
	Cz257	0.41	-0.16	-0.27	-0.29	-0.56
	Pz100	1.27	1.39	1.42	1.27	1.02
	Oz120	2.02	2.26	2.40	2.17	2.41
	M	1.61	1.14	1.07	1.12	1.01
Old	FPz30	2.17	2.12	1.70	2.10	2.38
	Fz15	1.71	1.04	1.42	1.37	2.06
	Cz257	1.32	0.78	1.23	1.17	1.76
	Pz100	1.19	0.93	1.18	1.17	1.80
	Oz120	1.04	1.18	1.26	1.24	1.92
	M	1.49	1.21	1.36	1.41	1.98

Table 6

.

Mean P3a Latencies (in milliseconds) at Site Fpz30 for Younger and Older Adults Including the Group Difference Score (Old minus Young).

	Task Condition				
	Positive	*Baseline*	*Familiar*	*Highly Familiar*	*Response Conflict*
Group					
Young	274 (19)	285 (31)	282 (20)	282 (19)	291 (29)
Old	365 (42)	353 (49)	345 (46)	346 (28)	339 (40)
Old –Young	91	68	63	64	48

Table 7.

Mean P3b Amplitudes for Each Condition and Age Group at Midline Sites.

		Task Condition				
		Positive	*Baseline*	*Familiar*	*Highly Familiar*	*Response Conflict*
Group	*Site*					
Young	FPz30	-0.95	-0.09	-1.23	-0.31	-1.11
	Fz15	-0.81	-0.31	-1.06	-0.97	-1.10
	Cz257	0.58	0.28	0.00	-0.23	-0.28
	Pz100	1.70	1.13	1.45	1.17	1.22
	Oz120	1.35	0.82	1.26	1.13	1.35
	M	0.37	0.37	0.08	0.16	0.02
Group	*Site*					
Old	FPz30	-0.38	-0.08	-0.12	0.17	0.12
	Fz15	0.98	1.06	1.01	0.99	1.32
	Cz257	1.23	1.05	1.04	0.97	1.35
	Pz100	1.21	0.62	1.01	0.84	1.13
	Oz120	0.35	-0.03	0.36	0.19	0.54
	M	0.68	0.52	0.66	0.63	0.89

Table 8.

Mean N450 Amplitudes for Each Condition and Age Group at Frontal-Midline Sites.

		Task Condition				
		Positive	*Baseline*	*Familiar*	*Highly Familiar*	*Response Conflict*
Group	*Site*					
Younger	FPz30	-1.40	-0.68	-1.37	-0.57	-1.41
	AFz21	-1.47	-1.06	-1.80	-1.53	-2.23
	Fz15	-1.05	-1.03	-1.60	-1.35	-1.96
	FCz8	-0.57	-0.90	-1.36	-1.10	-1.69
	Cz257	0.42	-0.40	-0.58	-0.58	-0.97
	M	-0.81	-0.81	-1.34	-1.03	-1.65
Older	FPz30	-0.28	0.08	-0.32	-0.02	0.04
	AFz21	0.85	0.70	0.65	0.69	0.88
	Fz15	1.17	0.99	0.91	0.83	1.18
	FCz8	1.43	1.18	1.05	0.94	1.42
	Cz257	1.27	0.93	0.85	0.79	1.17
	M	0.88	0.78	0.63	0.65	0.94

Table 9.

Mean N450 Amplitudes for Each Condition and Age Group at Lateral Sites.

		Task Condition				
		Positive	*Baseline*	*Familiar*	*Highly Familiar*	*Response Conflict*
Group	*Site*					
Younger	L38	-1.25	-1.05	-1.09	-1.23	-1.80
	AFz21	-1.47	-1.06	-1.80	-1.53	-2.23
	R03	-0.97	-0.71	-1.14	-0.83	-1.63
	M	-1.23	-0.94	-1.34	-1.20	-1.89
Older	L38	-0.05	0.41	-0.11	-0.12	0.08
	AFz21	0.85	0.70	0.65	0.61	0.88
	R03	0.45	0.40	0.45	0.06	0.60
	M	0.42	0.50	0.33	0.18	0.52

Table 10.

Mean Estimates of the Variance in the Topography of N450 Responses across Conditions.

	Task Condition				
	Positive	*Baseline*	*Familiar*	*Highly Familiar*	*Response Conflict*
Group					
Young	75.2	90.8	90.0	84.2	76.4
Old	79.3	105.4	94.6	106.9	84.2
Total	77.4	98.5	92.5	96.2	80.5

Table 11.

Mean Amplitudes of the Expanded N450 for each Condition and Age Group.

	Task Condition				
	Positive	*Baseline*	*Familiar*	*Highly Familiar*	*Response Conflict*
Group					
Young	-1.12	-0.46	-1.39	-0.91	-1.82
Old	0.50	0.54	0.36	0.41	0.68

Table 12 .

Correlations between residual variances from Trials B, Accuracy and Response Times from the Response Conflict trials and Response Conflict ERP components (residuals) in younger adults (N = 16) and older adults (N = 18).

		Component		
		P3a Res.	*P3b Res.*	*N450 Res.*
Group	*Measure*			
Younger	Trails B Residual	-.220	-.243	-.156
	RC Accuracy	-.059	.080	.236
	RC Resp. Time	-.027	-.032	-.492
Older	Trails B Residual	.075	.193	.174
	RC Accuracy	-.346	-.174	-.338
	RC Resp. Time	-.113	-.032	-.034

Note. * $p = < .05$; ** $p < .01$; *** $p < .001$

Table 13.
Correlations between recorded ERP components (residuals) from the positive, familiar and response conflict conditions for younger adults (N = 16) and older adults (N=18).

		Component		
		P3a Res.	*P3b Res.*	*N450 Res.*
Positive Condition				
Group	*Measure*			
Younger	P3a Res.	-	.499*	.267
	P3b Res.		-	.295
	N450 Res.			-
Older	P3a Res.	-	.487*	.190
	P3b Res.		-	.015
	N450 Res.			-
Familiar Condition				
Group	*Measure*			
Younger	P3a Res.	-	.704**	.390
	P3b Res.		-	.796**
	N450 Res.			-
Older	P3a Res.	-	.435	.724**
	P3b Res.		-	.295
	N450 Res.			-
Response Conflict Condition				
Group	*Measure*			
Younger	P3a Res.	-	.480	.128
	P3b Res.		-	.731**
	N450 Res.			-
Older	P3a Res.	-	.270	.520*
	P3b Res.		-	.256
	N450 Res.			-

Note. * $p = < .05$; ** $p < .01$, *** $p < .001$

Figure 1. Location of inferior frontal gyrus (IFG) in inferior frontal cortex and anterior cingulate cortex (ACC) in medial frontal cortex. Adopted from Nelson and colleagues 2003.

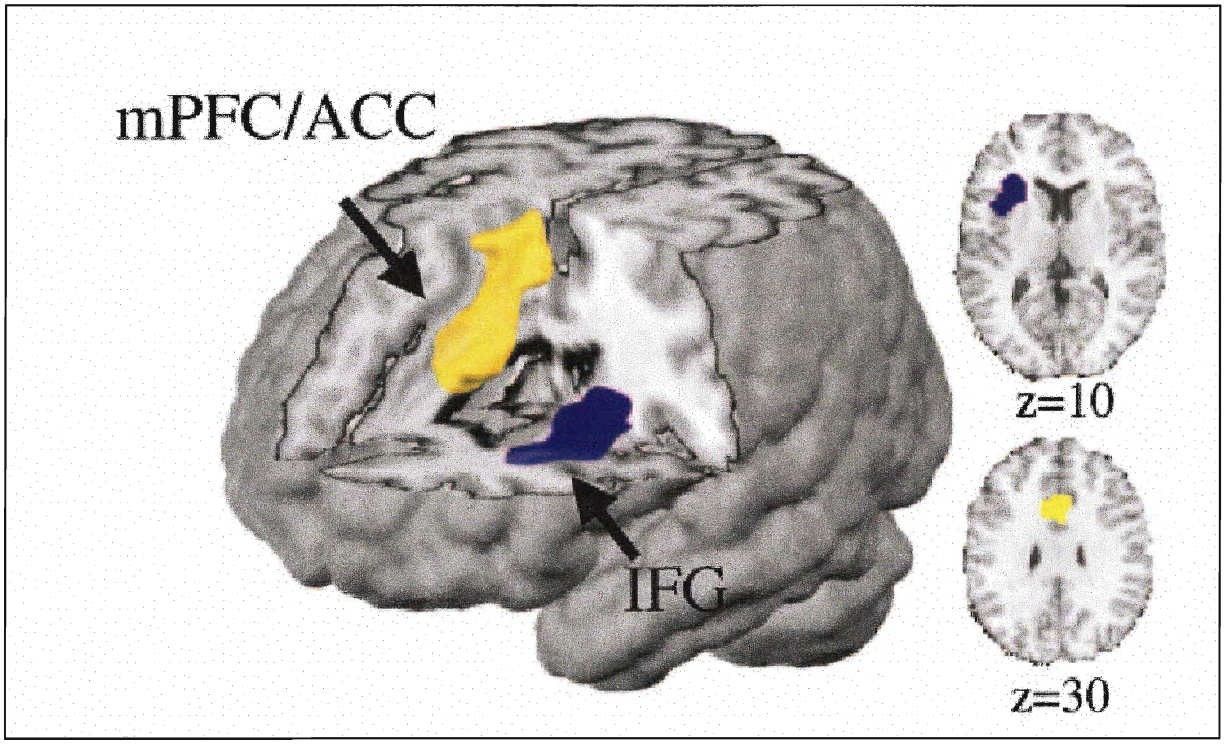


Figure 2. Examples of conditions in the Sternberg task. Colours are shown to highlight task manipulations.

	Target Set		Probe		Probe Type
Trial n-2	**p c r m**		**X**		
Trial n-1	**r b k h**		**H**		
Trial n	**q v s k**	if -	**S**	>	**Positive Response**
		if -	**F**	>	**Baseline**
		if -	**B**	>	**Negative/Familiar**
		if -	**R**	>	**Negative/ Highly Familiar**
		if -	**H**	>	**Negative/Response Conflict**

Figure 3. Overview of the EGI 256 channel montage with frontal electrodes facing the top of the figure ("Ref" = Cz 257)

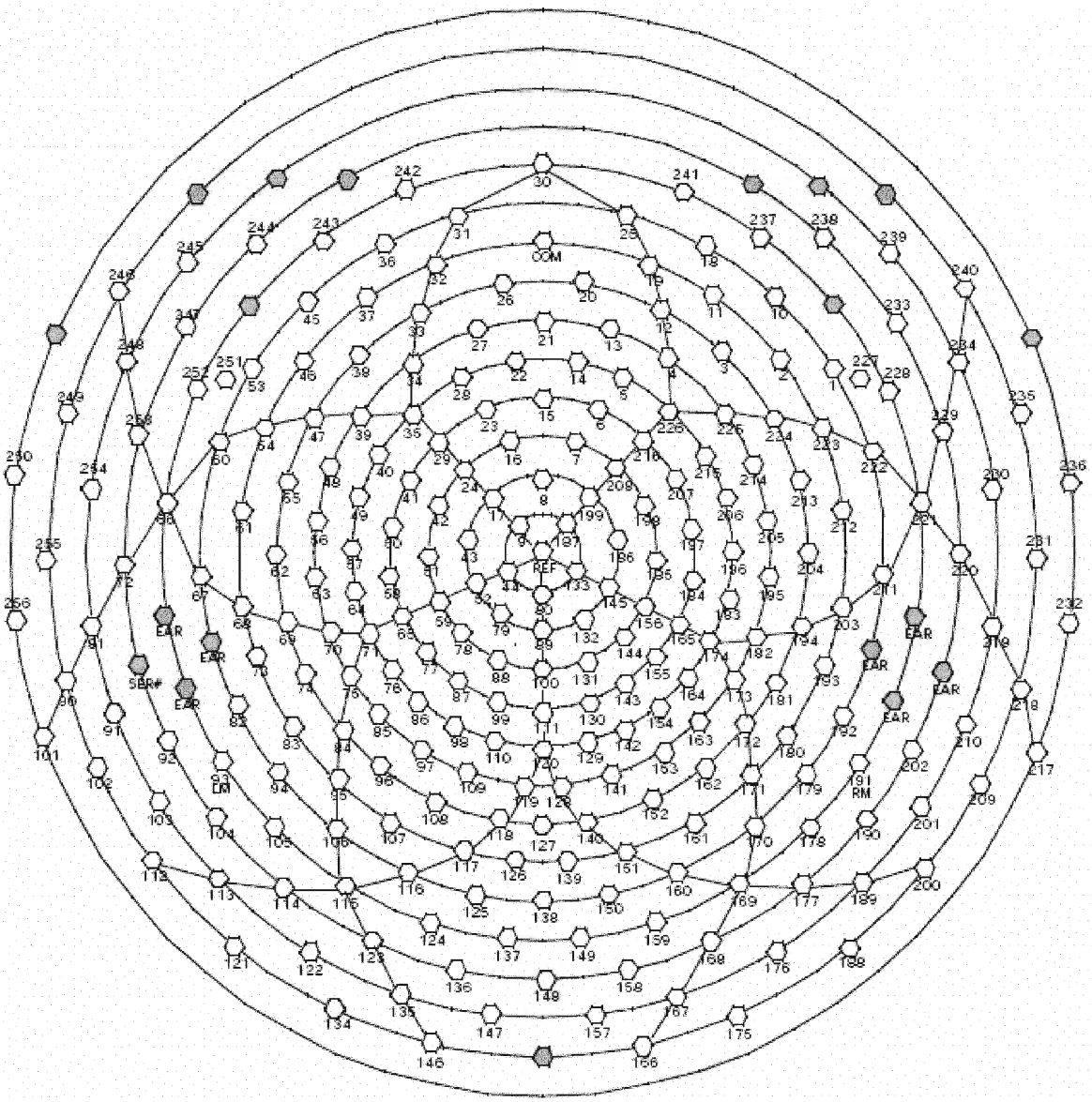


Figure 4. Mean accuracy for younger and older adults displayed for each condition of the Sternberg task.

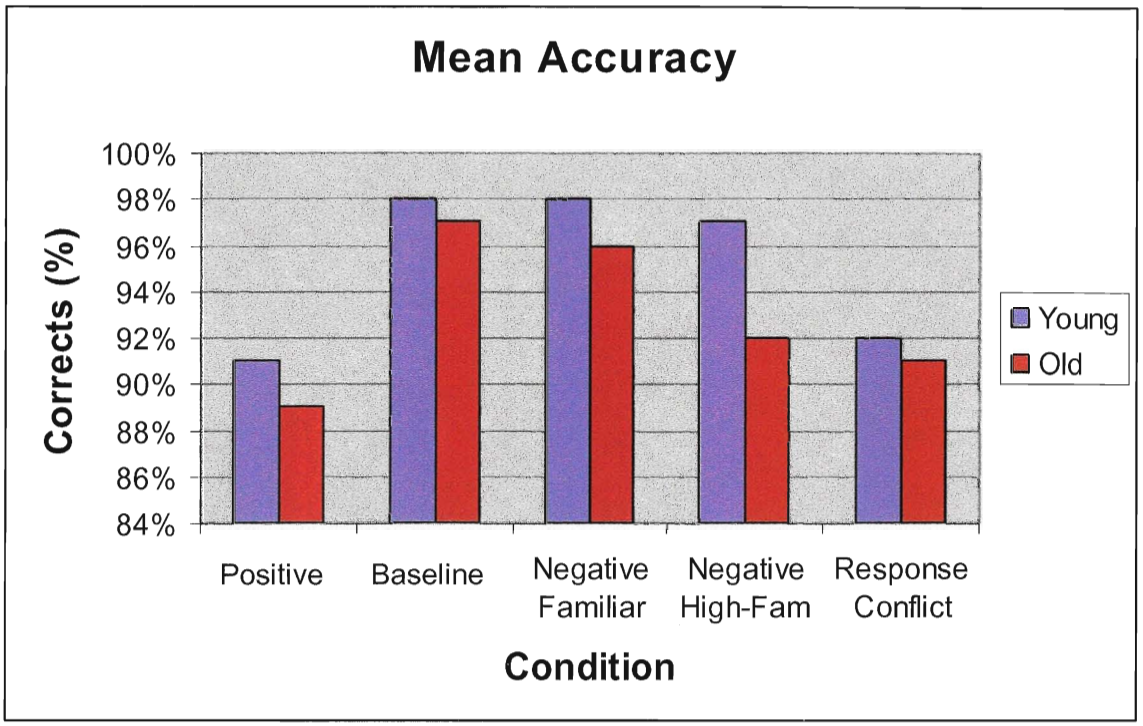


Figure 5. Mean response times for the younger and older adults displayed by each condition in the Sternberg task.

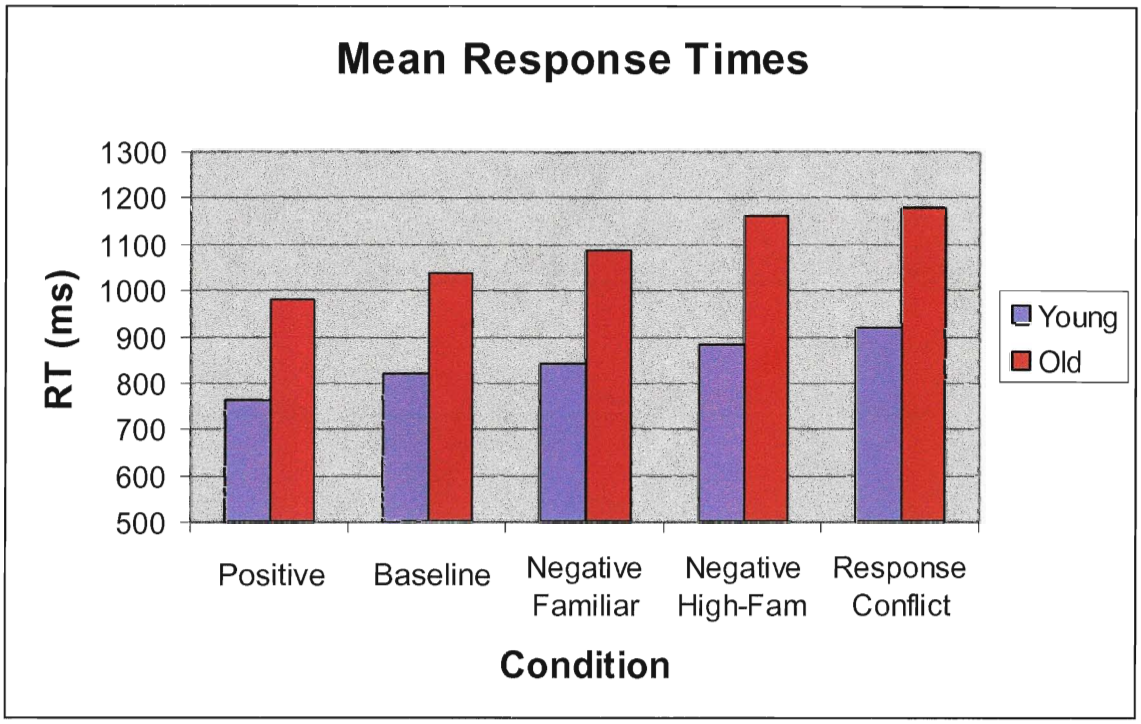


Figure 6a. Group averaged waveforms for the Positive and Baseline Condition for younger participants at midline sites.

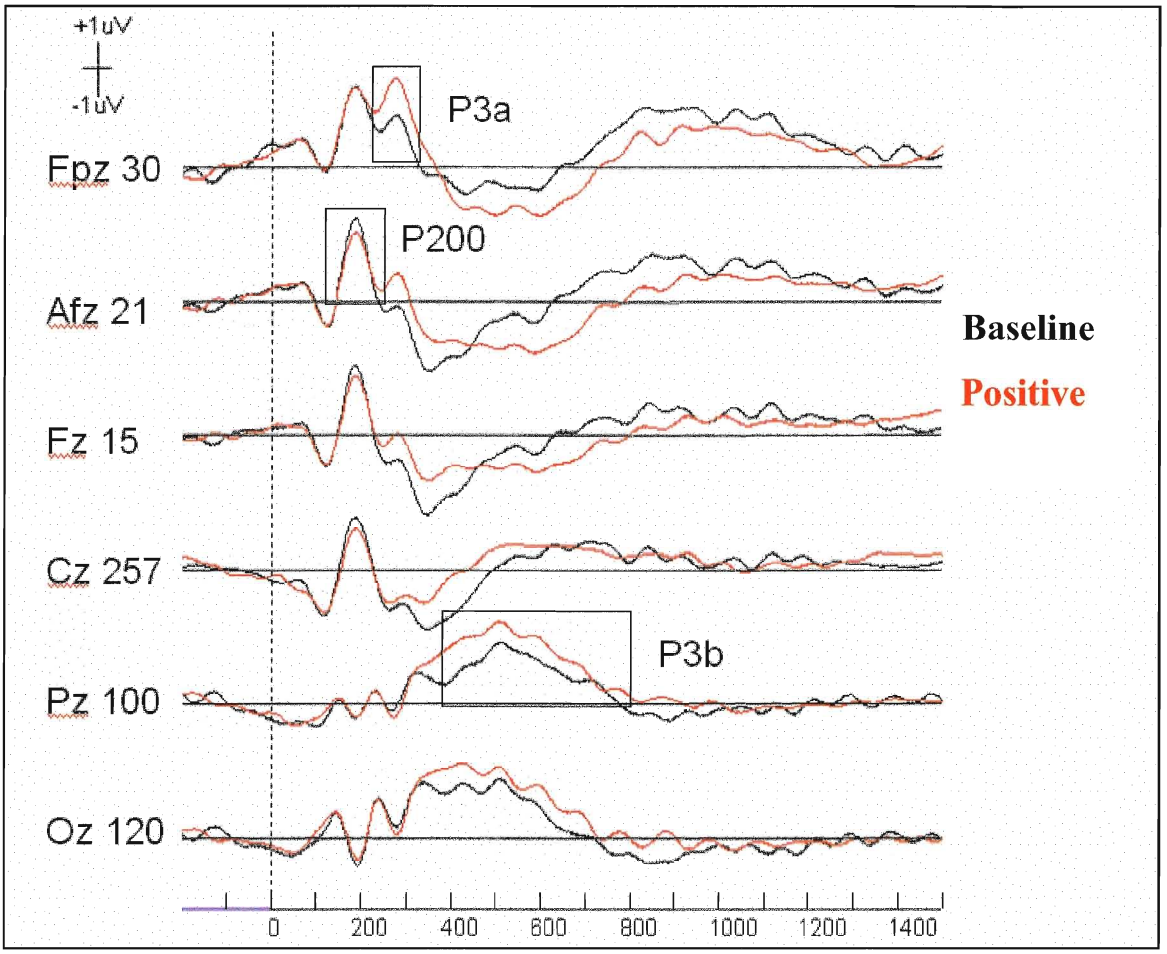


Figure 6b. Group averaged waveforms of Negative Conditions for younger participants at midline sites.

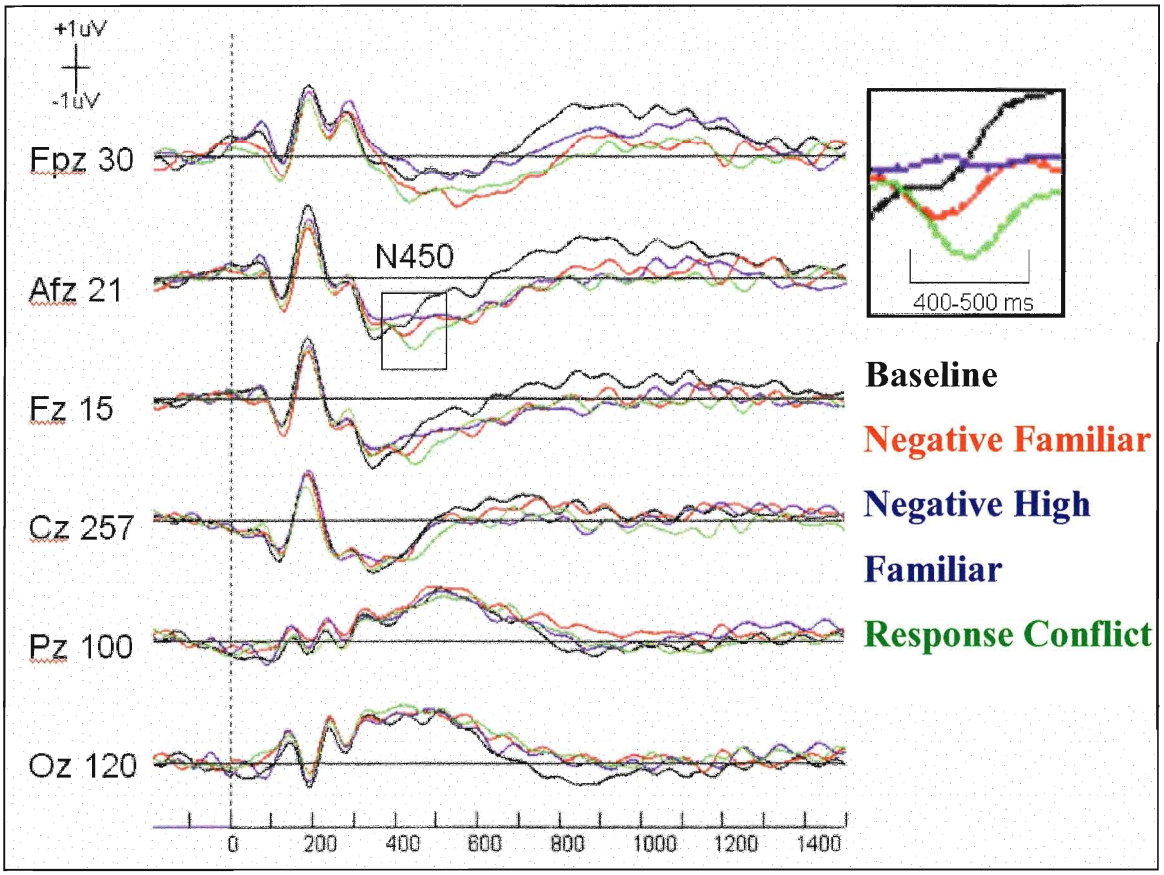


Figure 7a. Group averaged waveforms of the Positive and Baseline Conditions for older participants at midline sites.

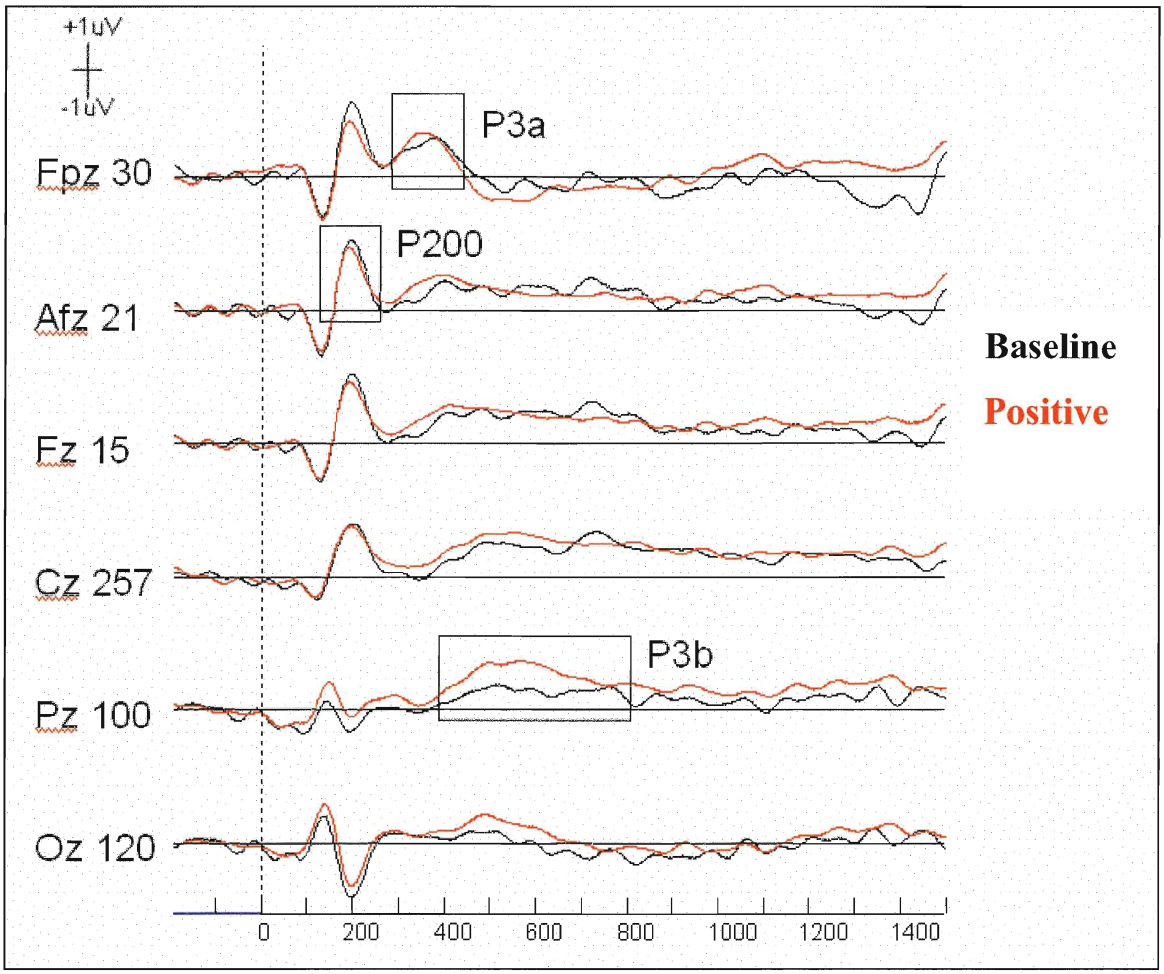


Figure 7b Group averaged waveforms of the Negative Conditions for older participants at midline sites.

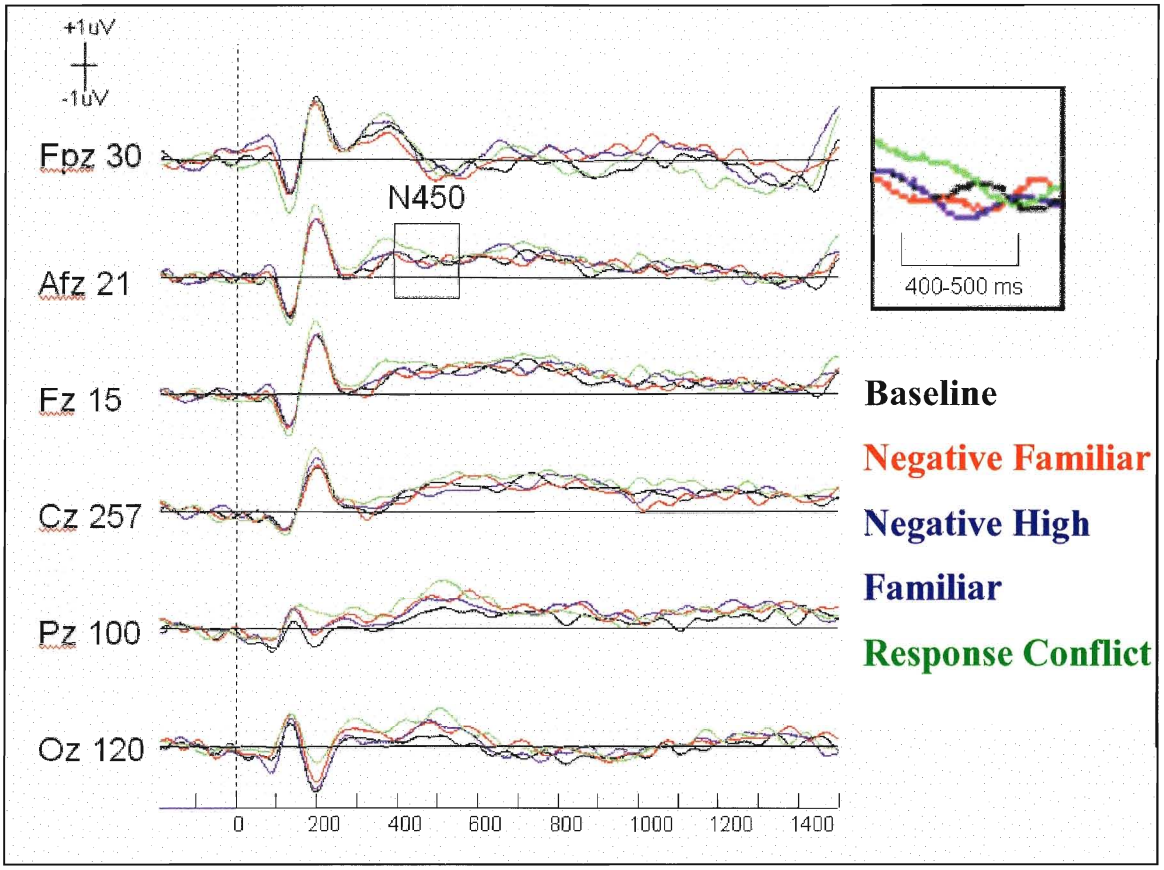
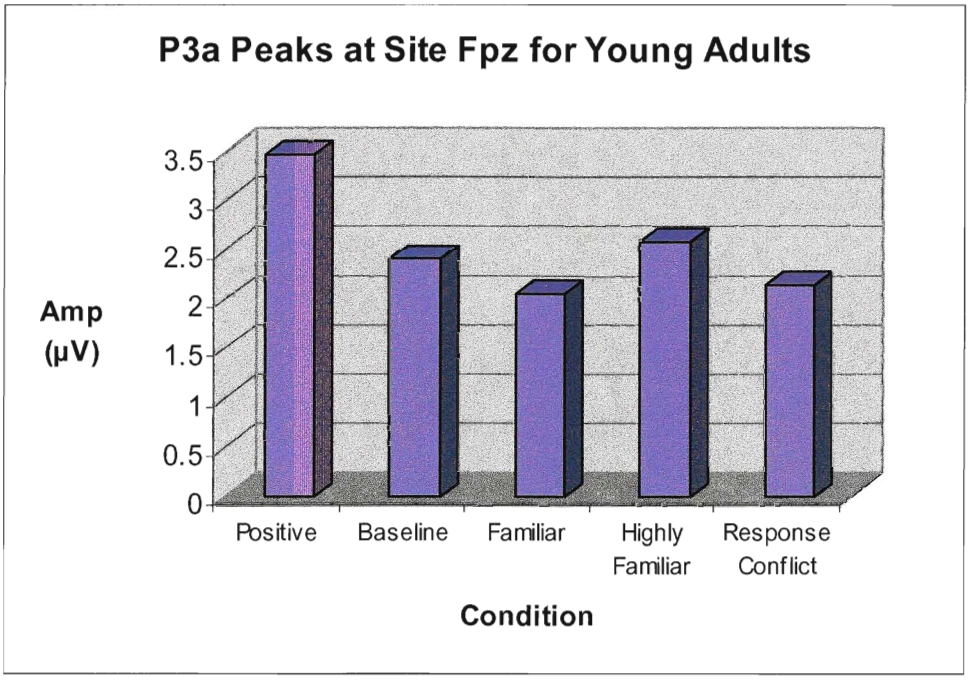


Figure 8. Mean peak amplitudes of the P3a component at site Fpz for younger and older adults.



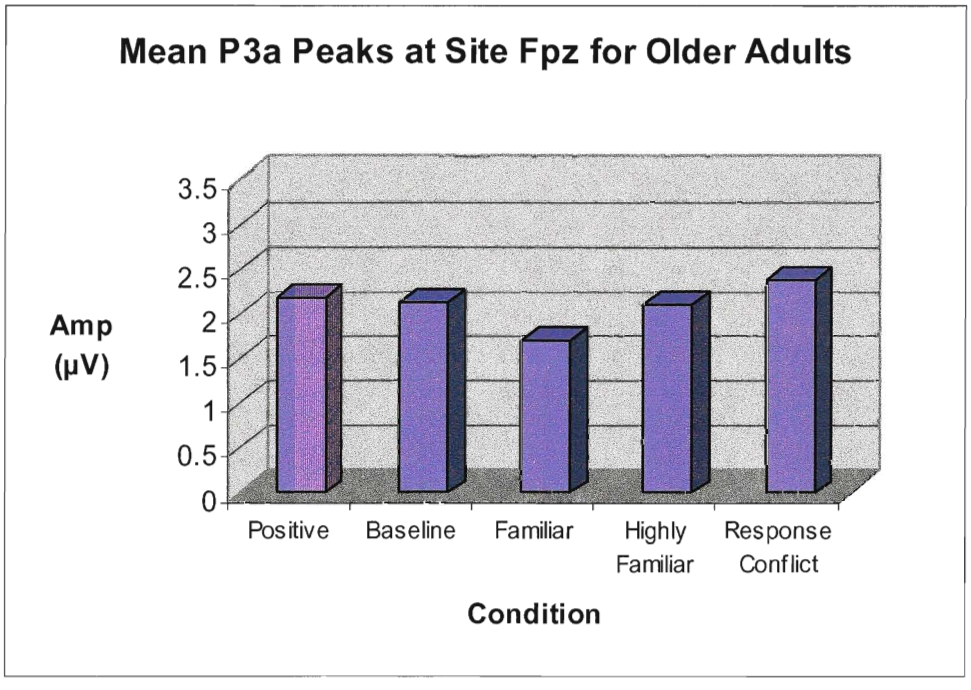
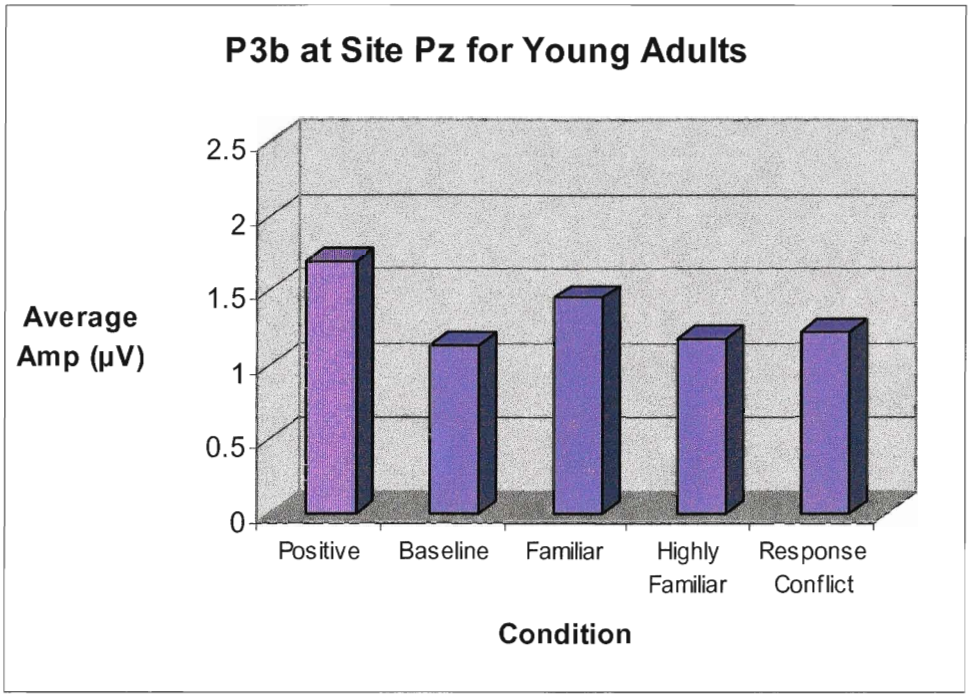


Figure 9. Mean peak amplitudes of the P3b component at site Pz for younger and older adults.



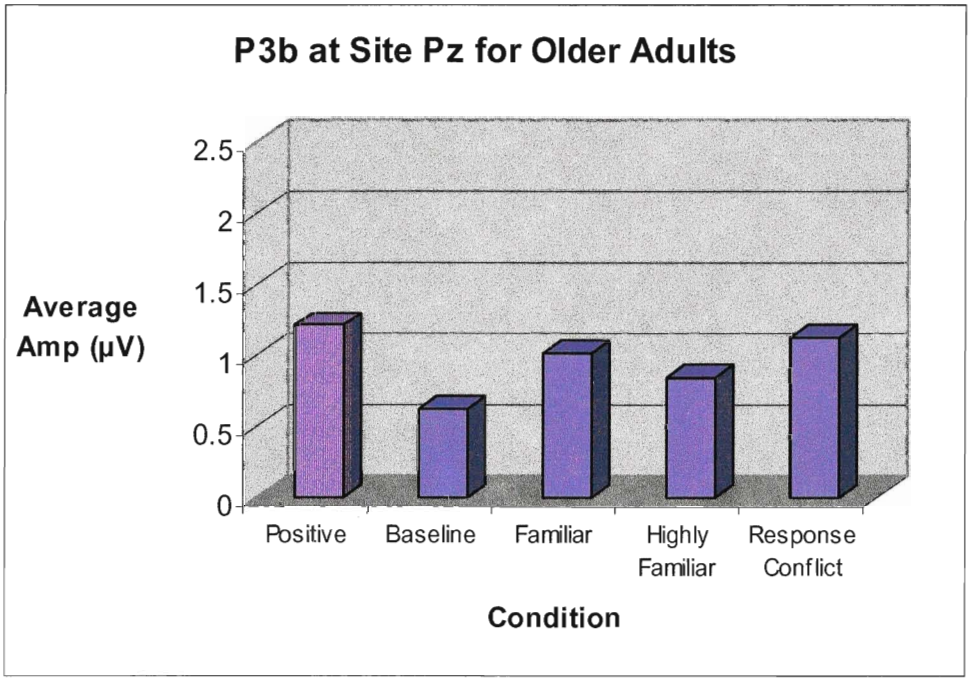
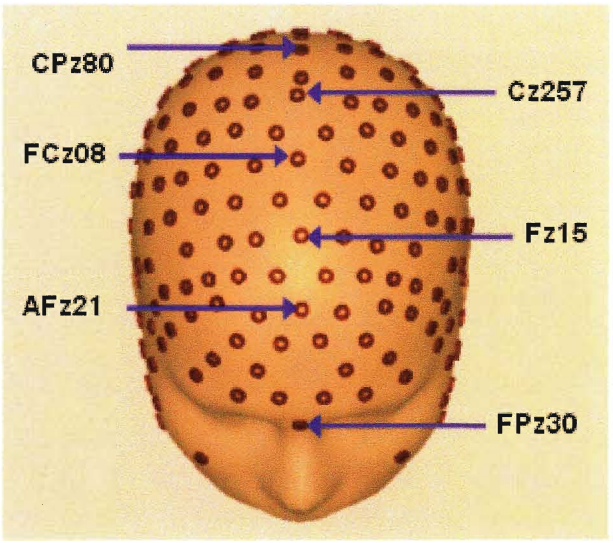
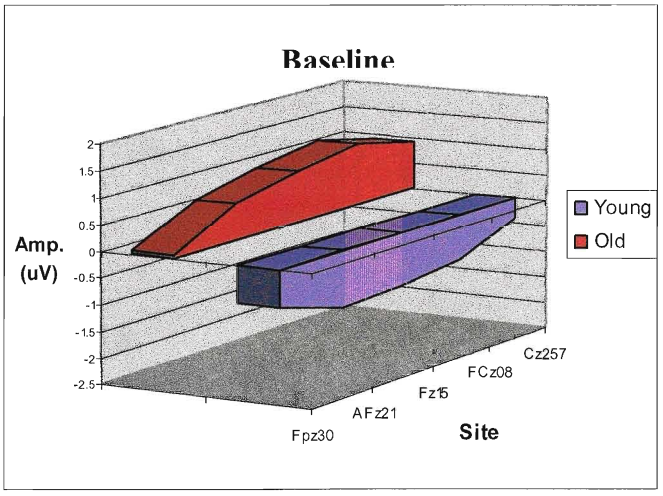
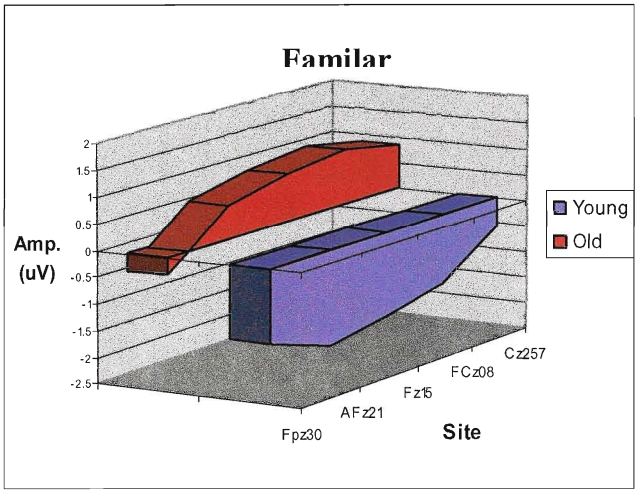
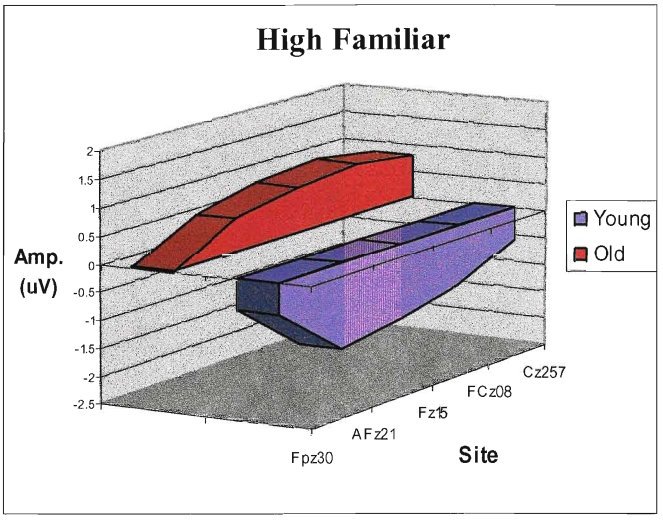


Figure 10. Mean amplitudes of the N450 at frontal-midline sites.









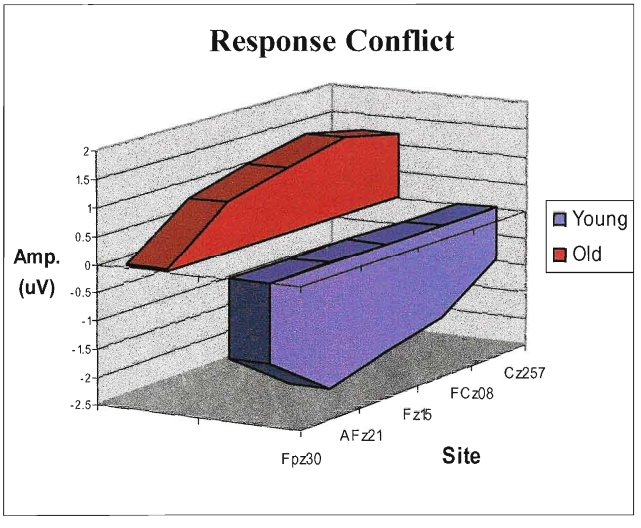
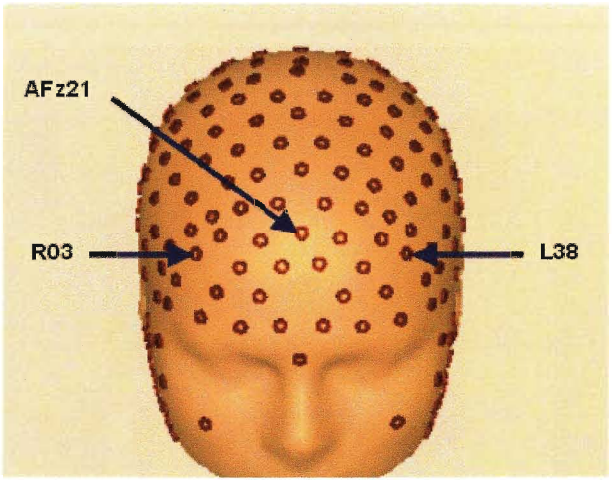
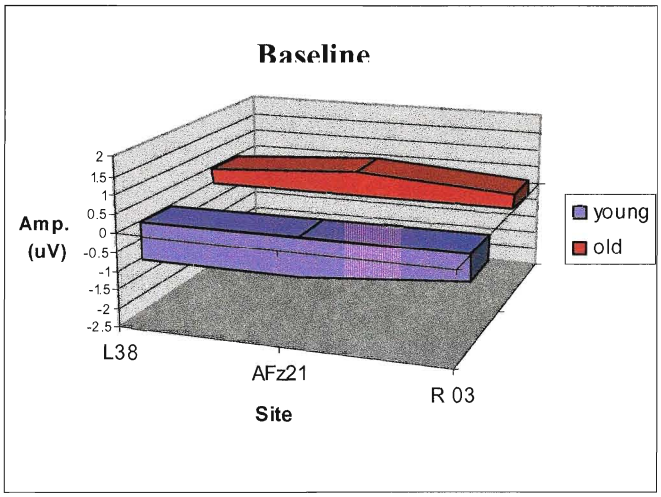
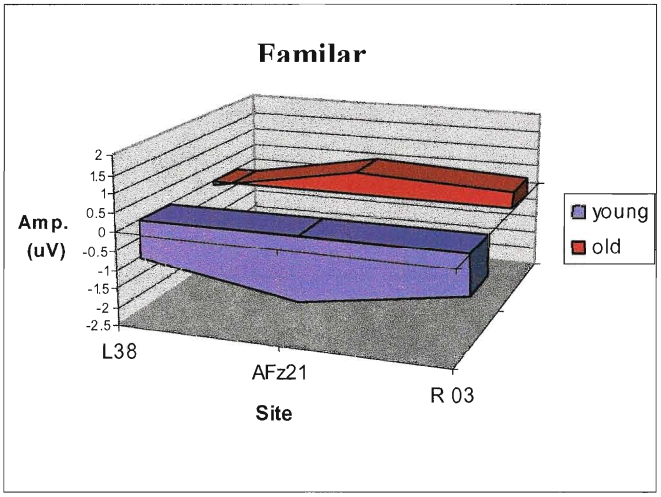
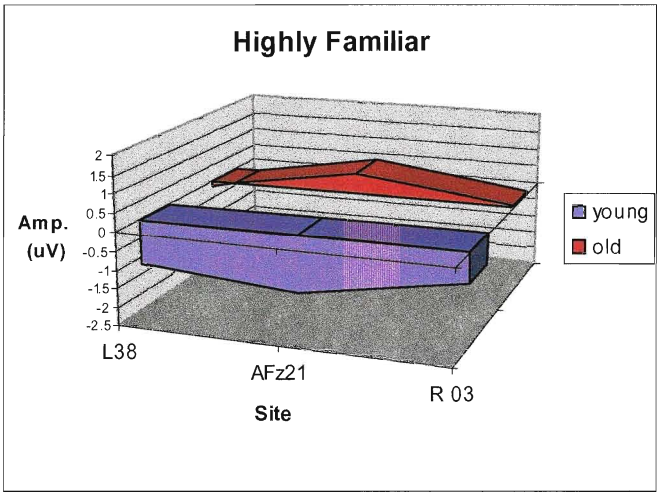


Figure 11. Mean amplitudes of the N450 at midline site AFz21 and lateral sites R03 and L38.









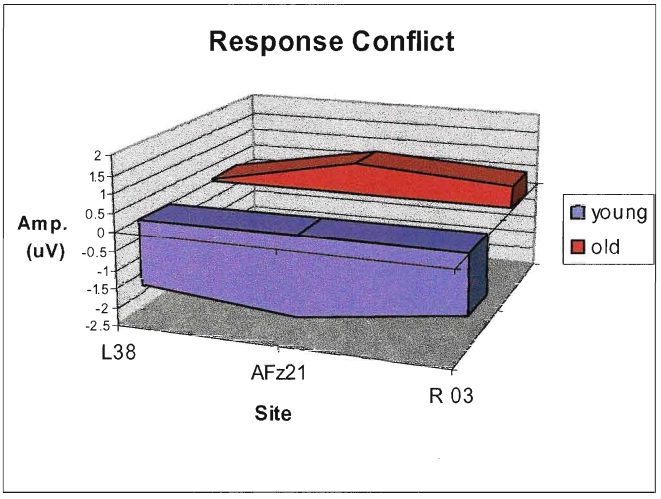


Figure 12. Mean Amplitudes of N450 Component at Site AFz21 Across Conditions for Each Age Group.

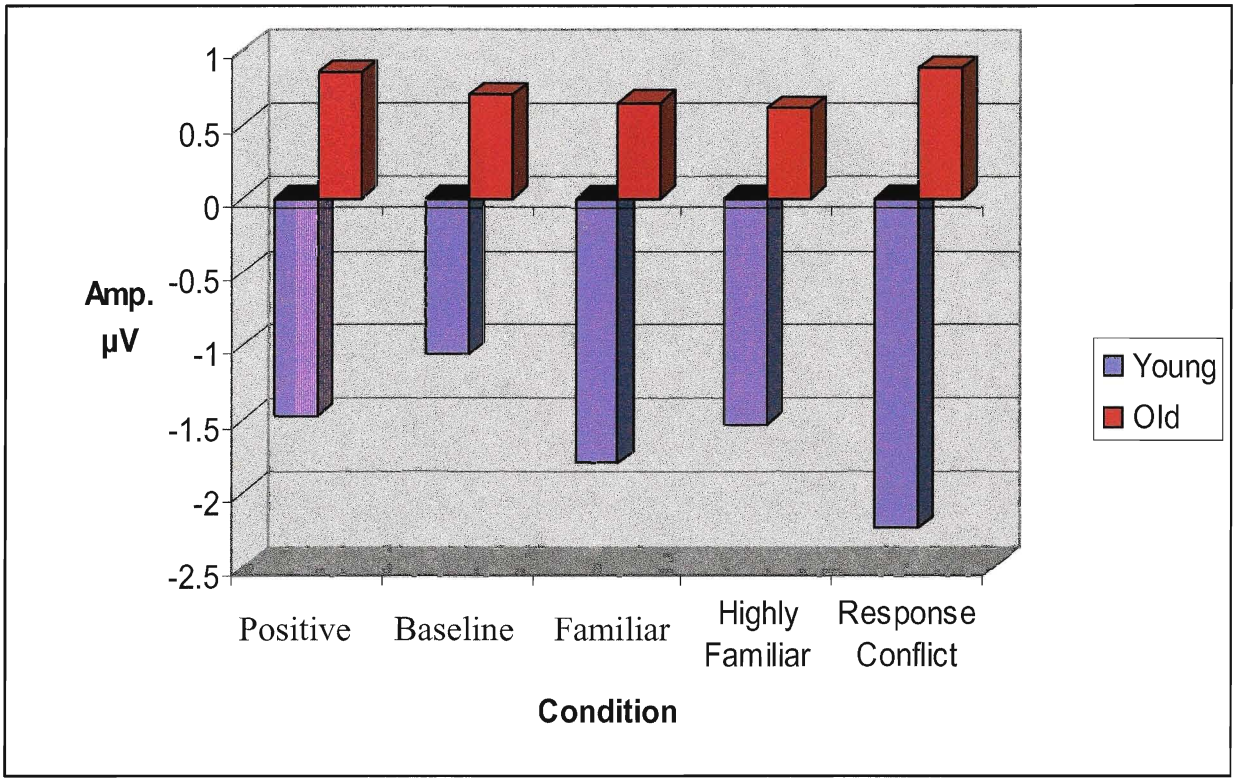


Figure 13. Scalp Topographies from the Baseline Condition for Both Younger and Older Adults from 400-500ms.

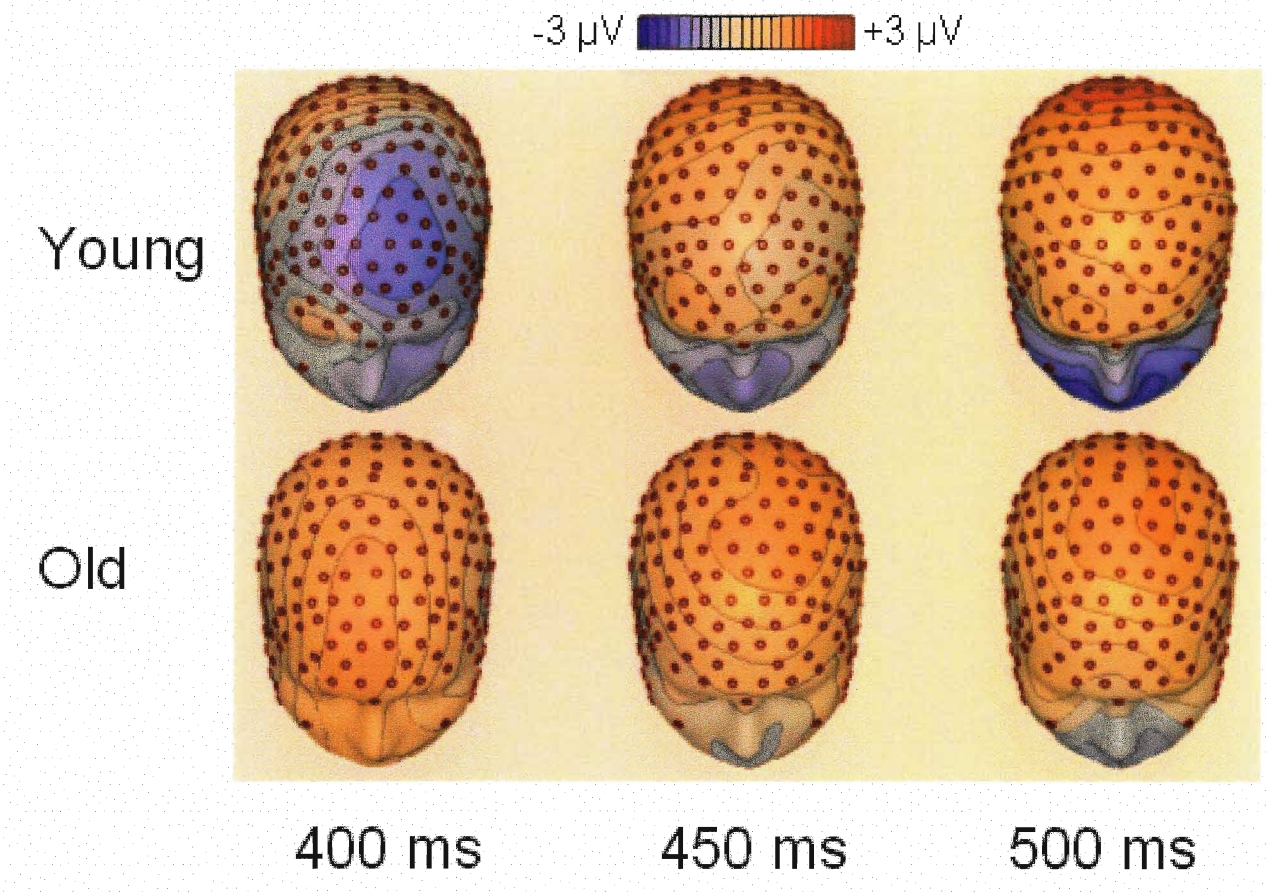


Figure 14. Scalp Topographies from the Familiar Condition for Both Younger and Older Adults from 400-500ms.

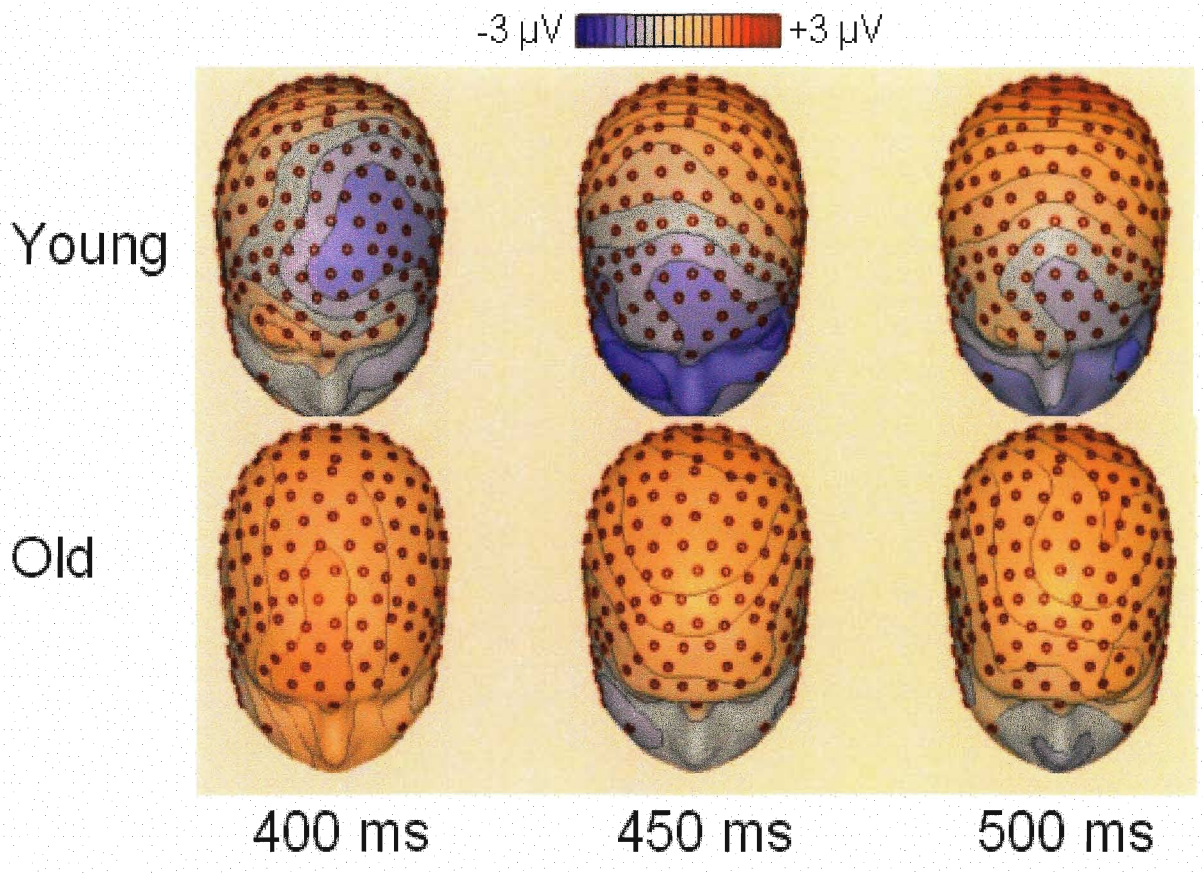


Figure 15. Scalp Topographies from the High Familiar Condition for Both Younger and Older Adults from 400-500ms.

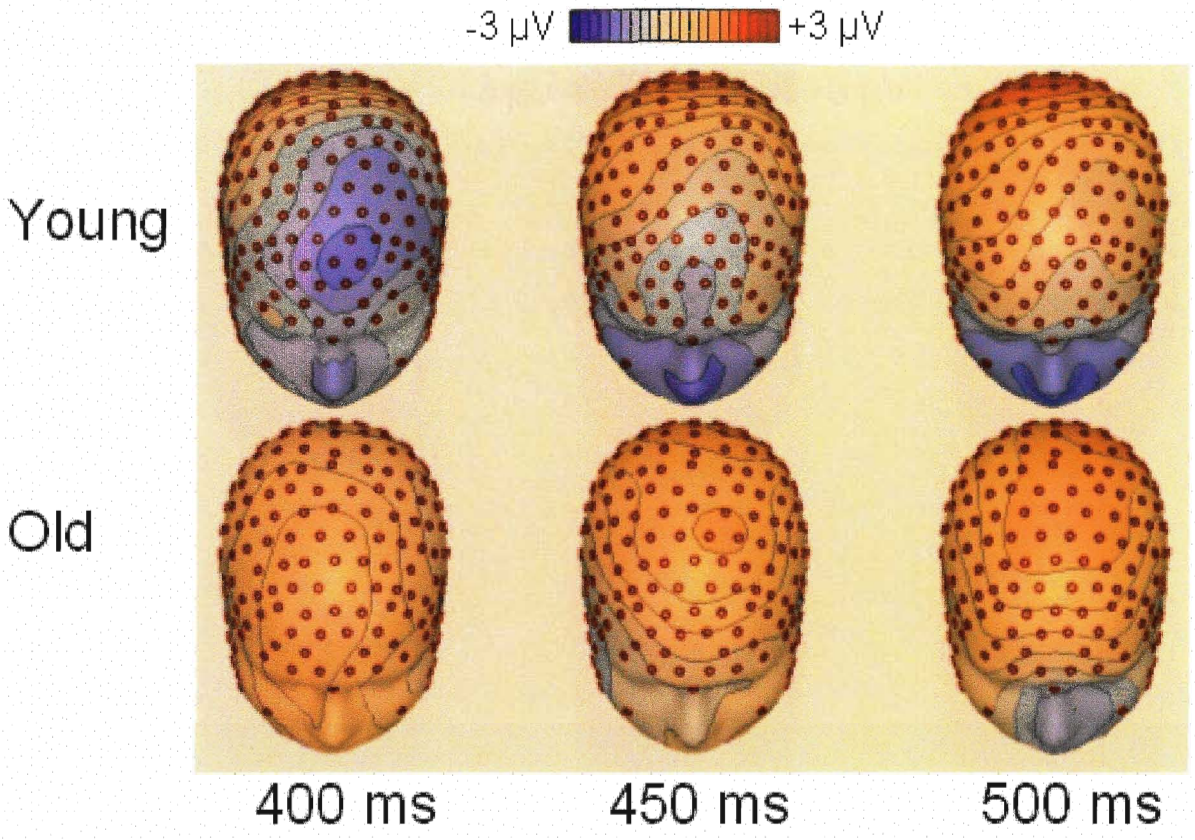


Figure 16. Scalp Topographies from the Response Conflict Condition for Both Younger and Older Adults from 400-500ms.

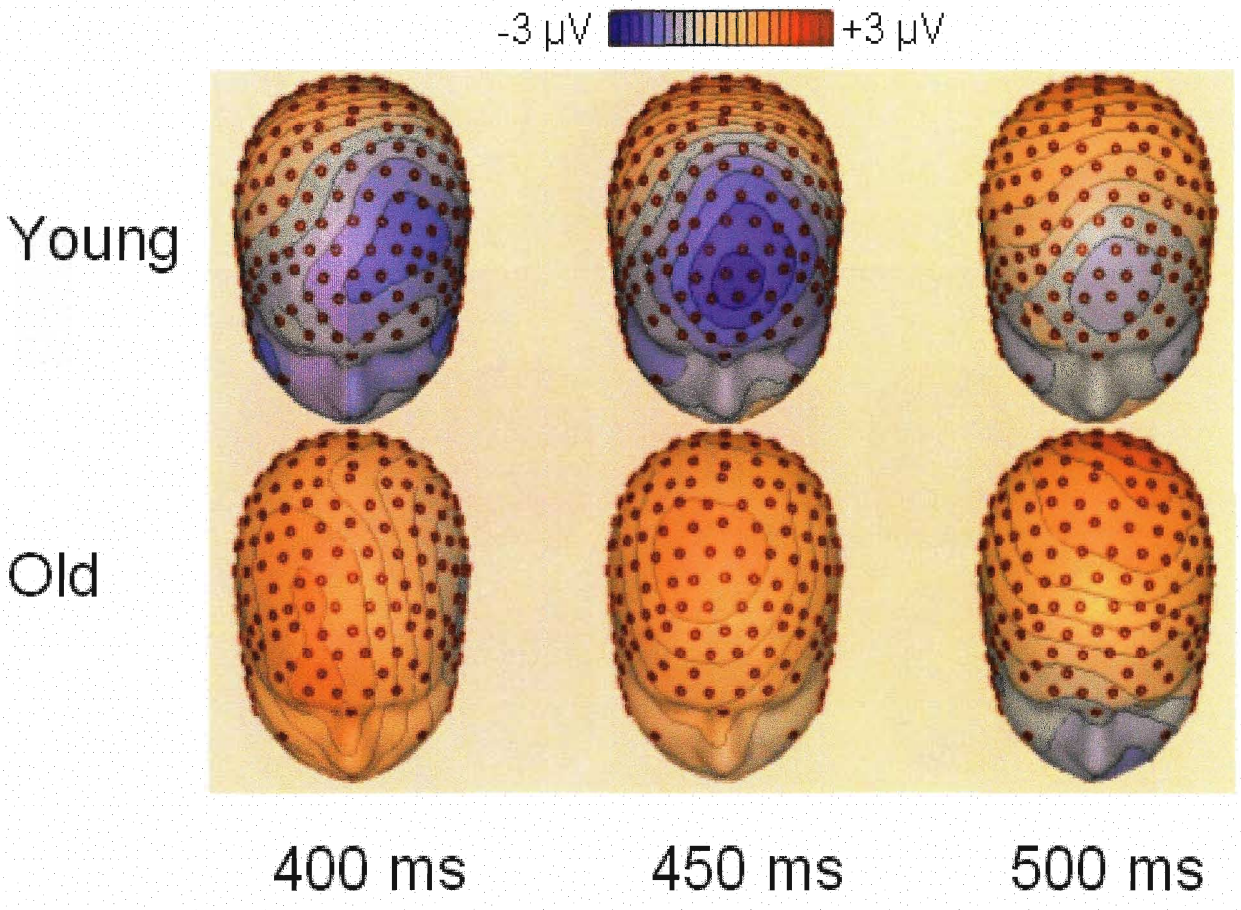


Figure 17. The Average Scalp Topography from 400-500 ms for Younger Adults (at the top of the figure) in the Response Conflict Condition Along with the 16 Individual Topographies Forming the Average (below).

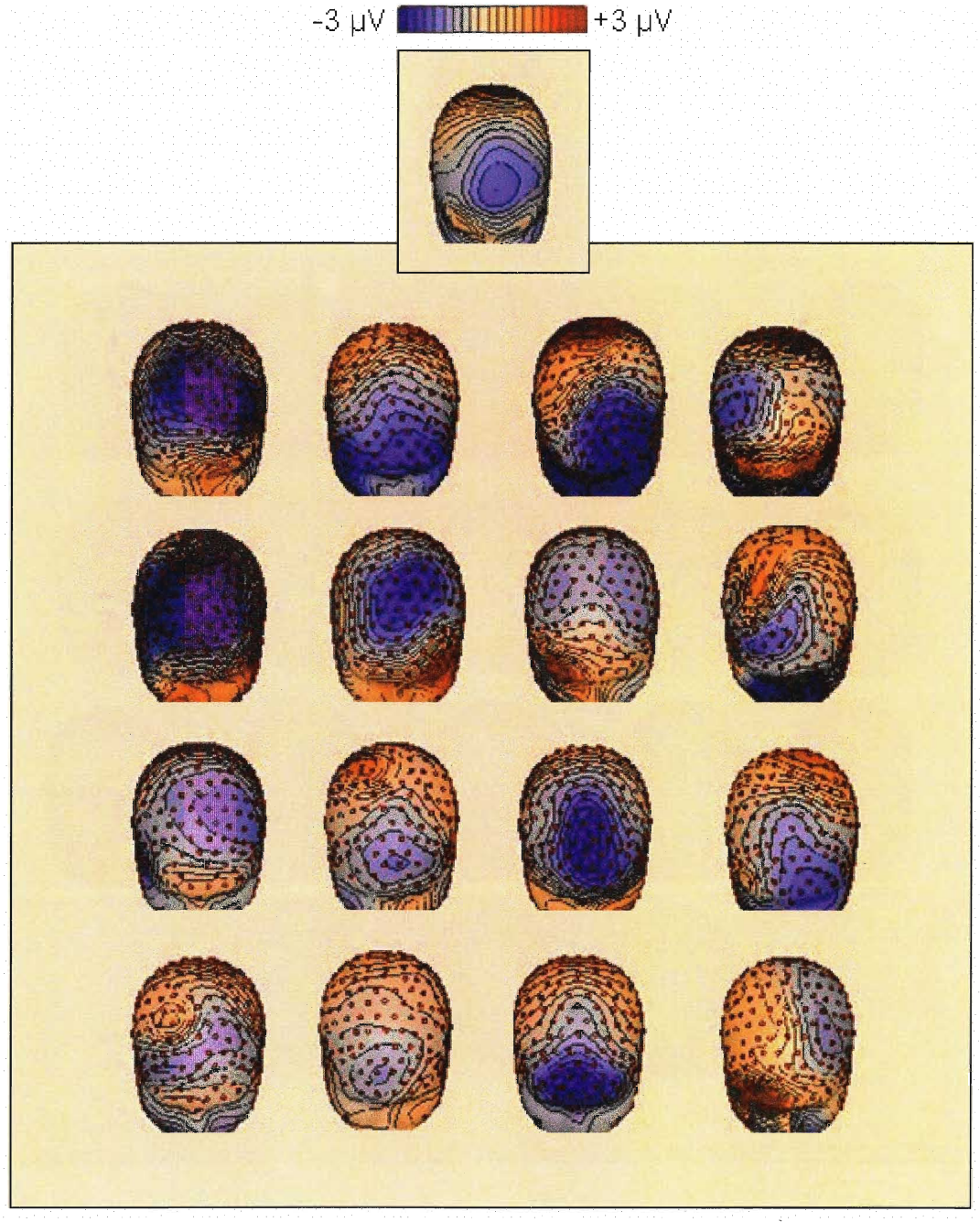


Figure 18. The Average Scalp Topography from 400-500 ms for Older Adults (at the top of the figure) in the Response Conflict Condition Along with the 18 Individual Topographies Forming the Average (below).

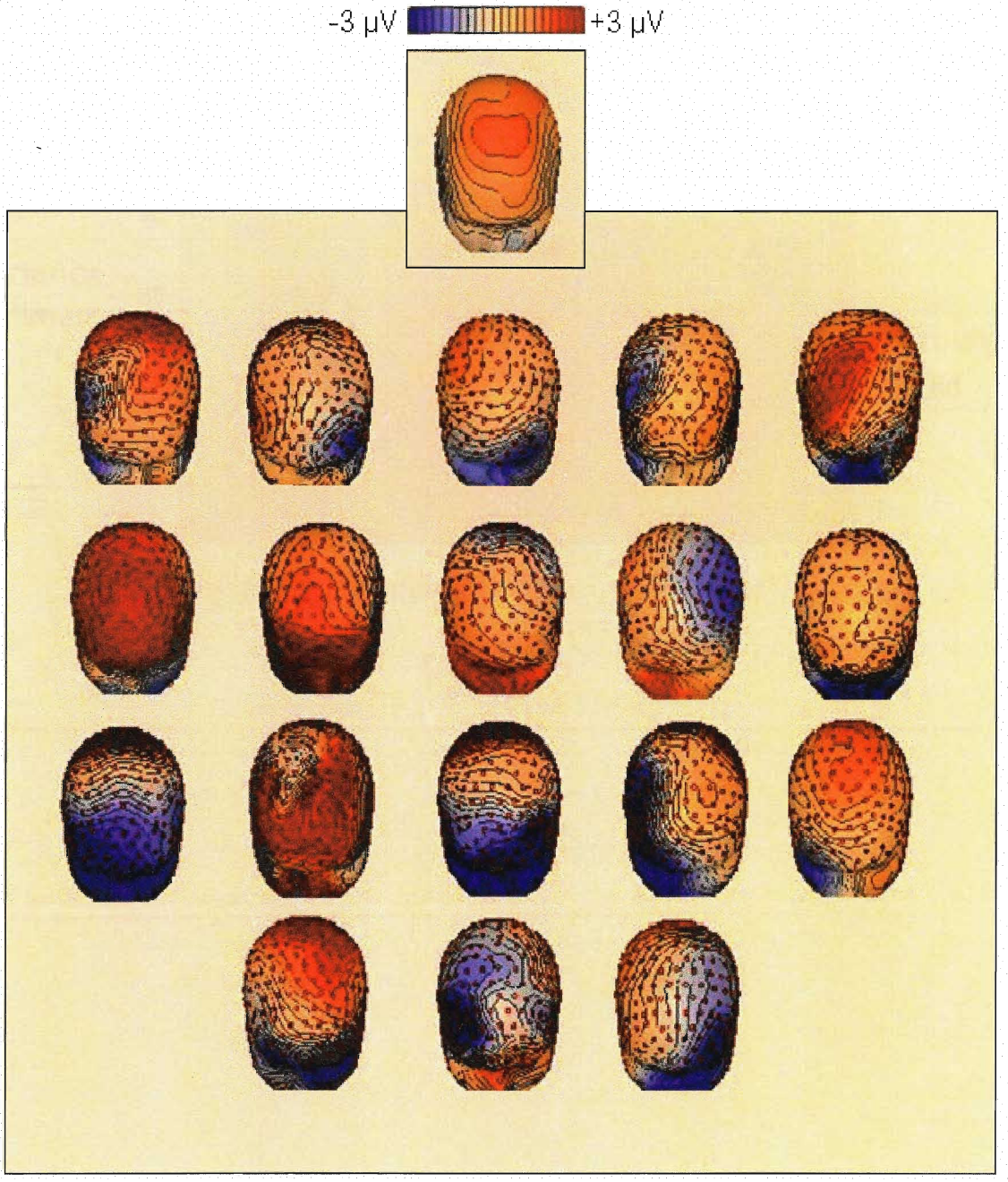


Figure 19. Estimates of N450 Topographical Variance Across the Negative Conditions for Each Age Group.

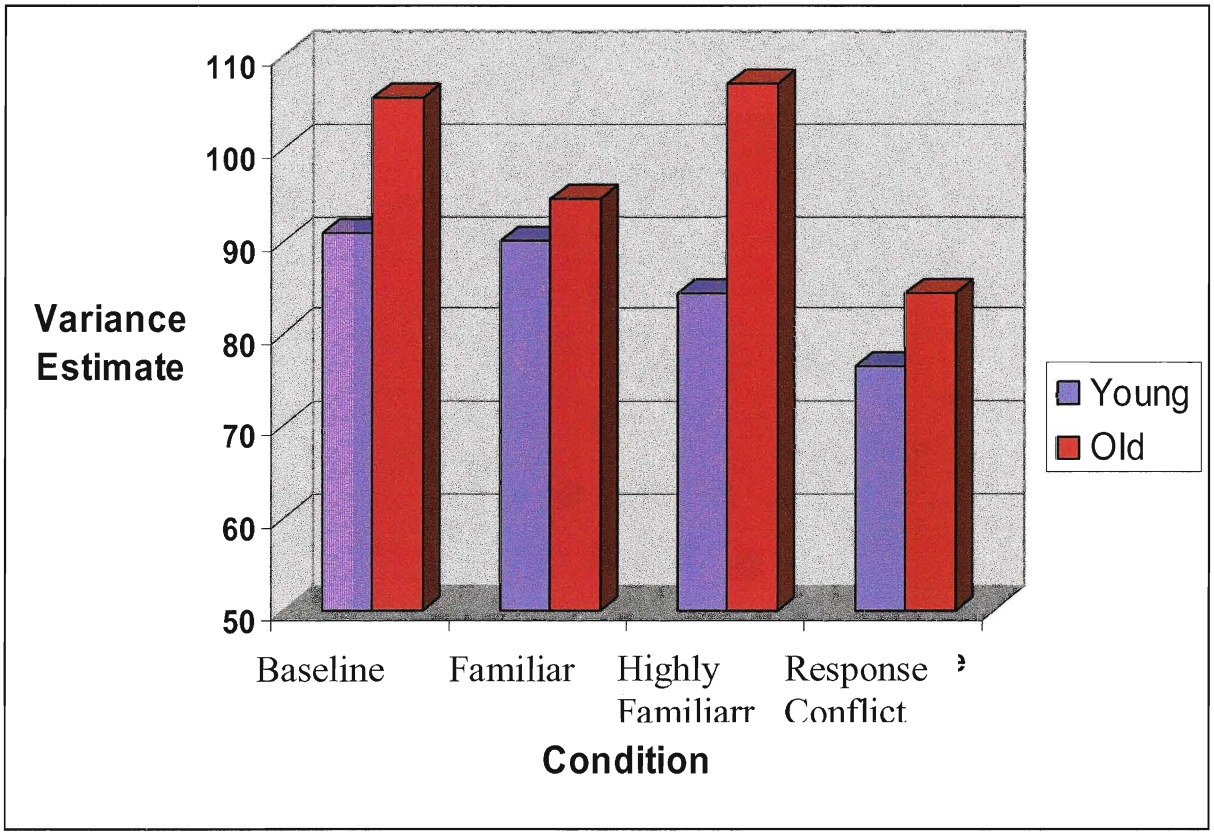


Figure 20. A Display of the Electrode Locations (in Blue) Constituting the Expanded N450 including sites 04, 05, 06, 12, 13, 14, 15, 19, 20, 21, 22, 23, 25, 26, 27, 28, 31, 32.

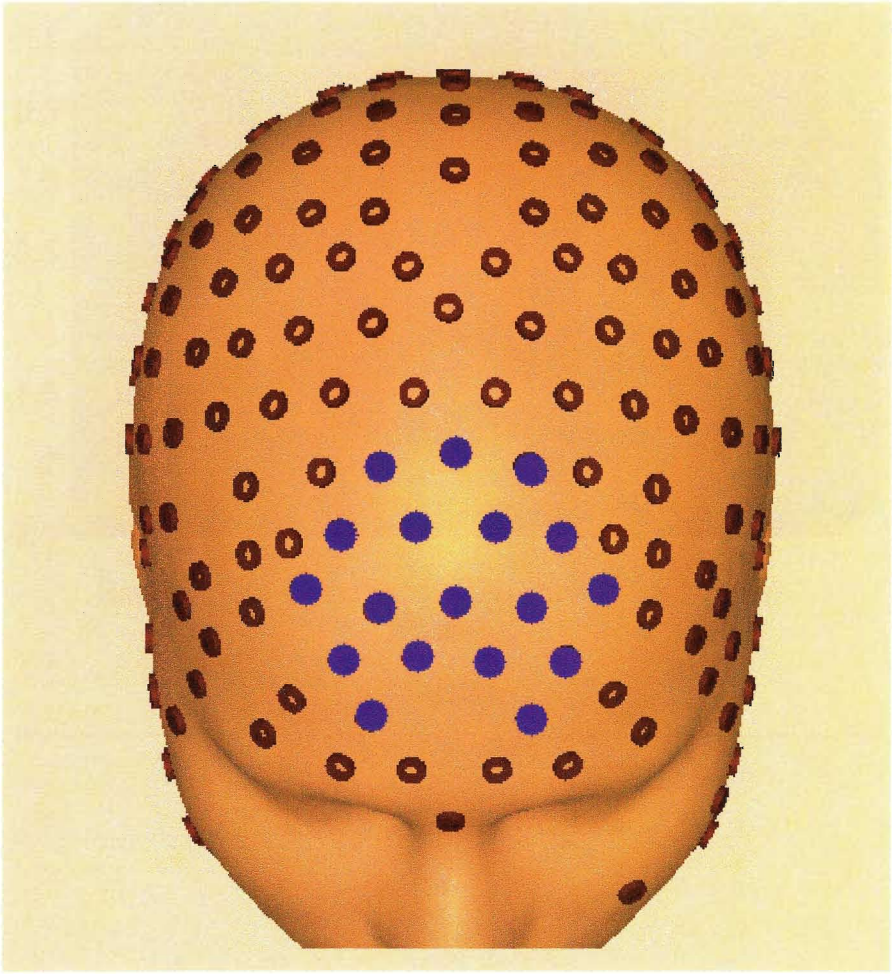


Figure 21. Mean Amplitudes of the Expanded N450 Component Across the Negative Conditions for Each Age Group.

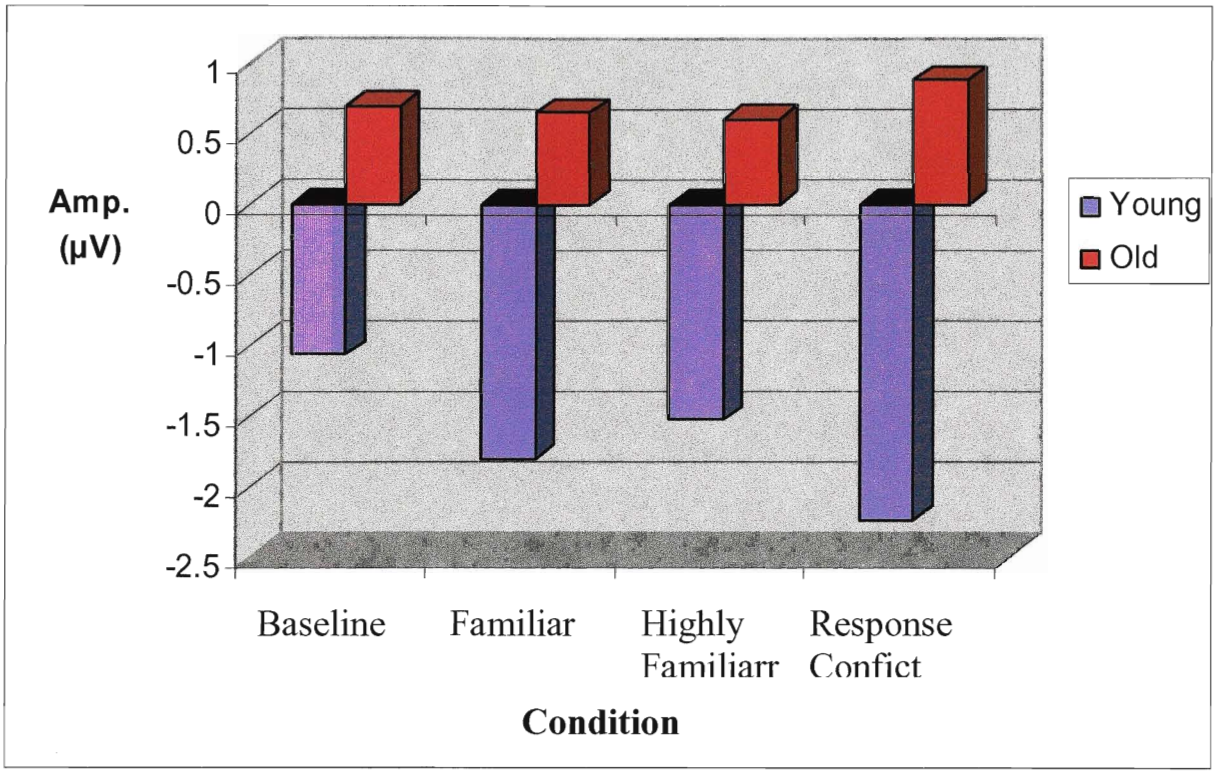


Figure 22a. Scatter plot of the relationship between the P3a and P3b standardized residuals of younger adults in the Positive condition (r = .499).

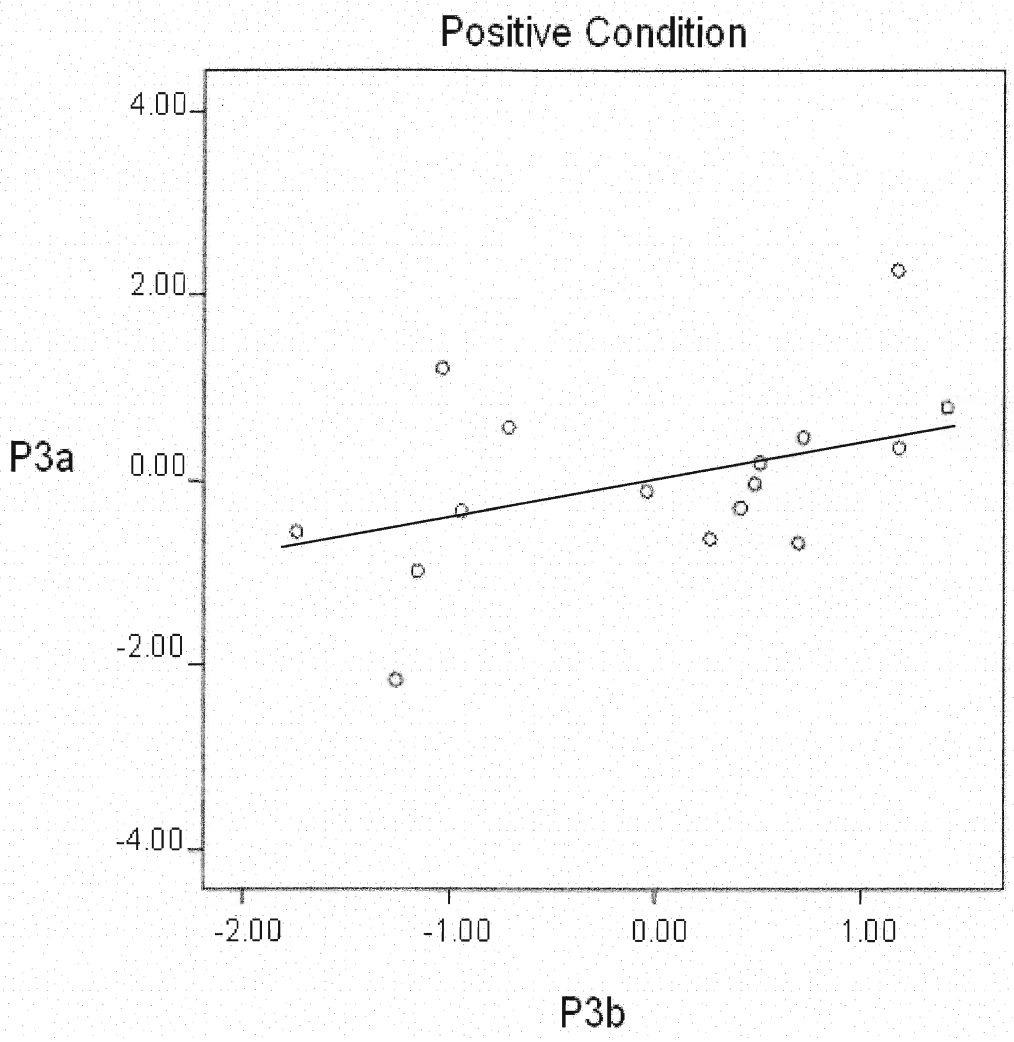


Figure 22b. Scatter plot of the relationship between the P3a and P3b standardized residuals of younger adults in the Familiar condition (r = .704).

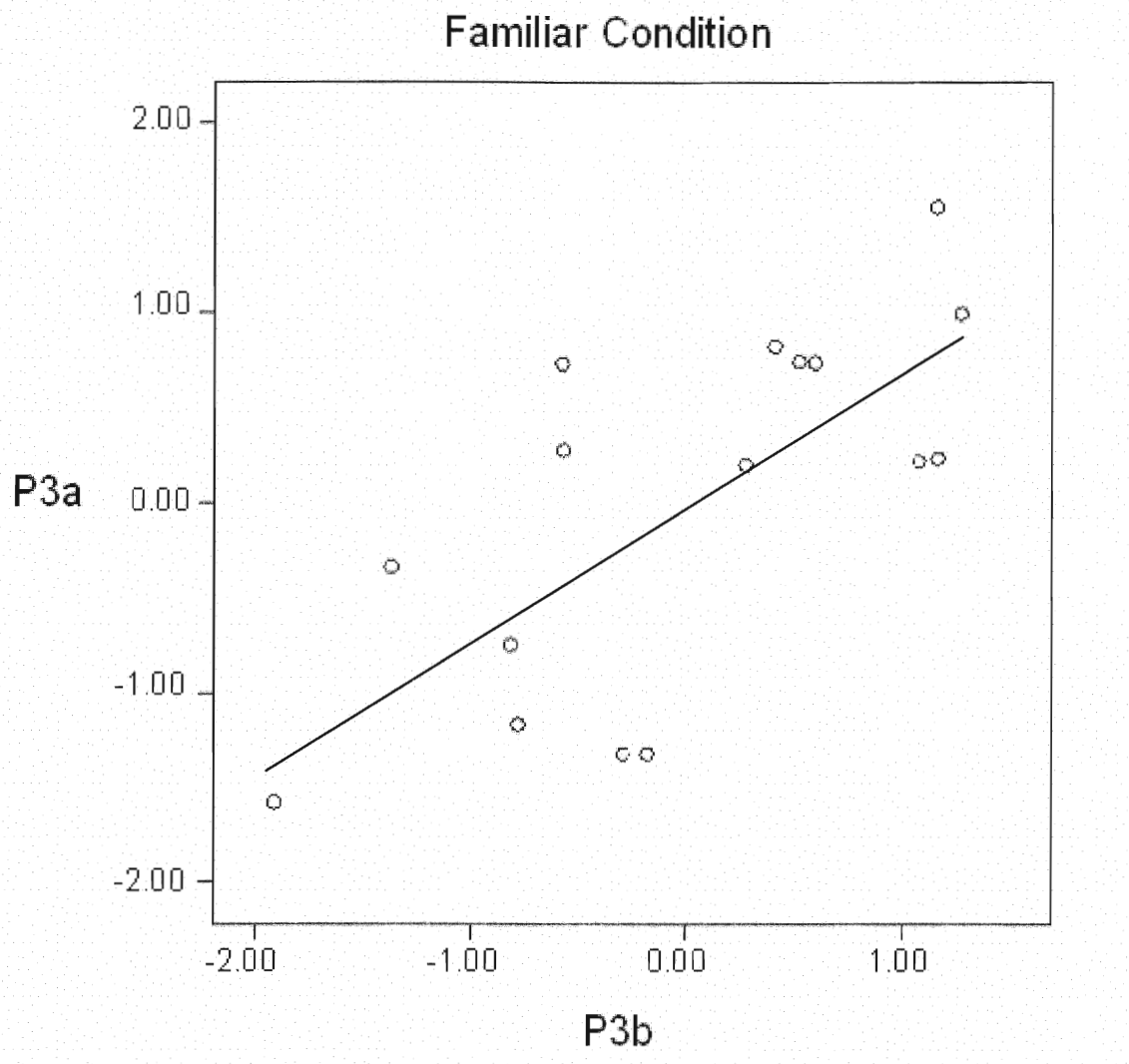


Figure 22c. Scatter plot of the relationship between the P3a and P3b standardized residuals of younger adults in the Response Conflict condition (r = .480, ns.).

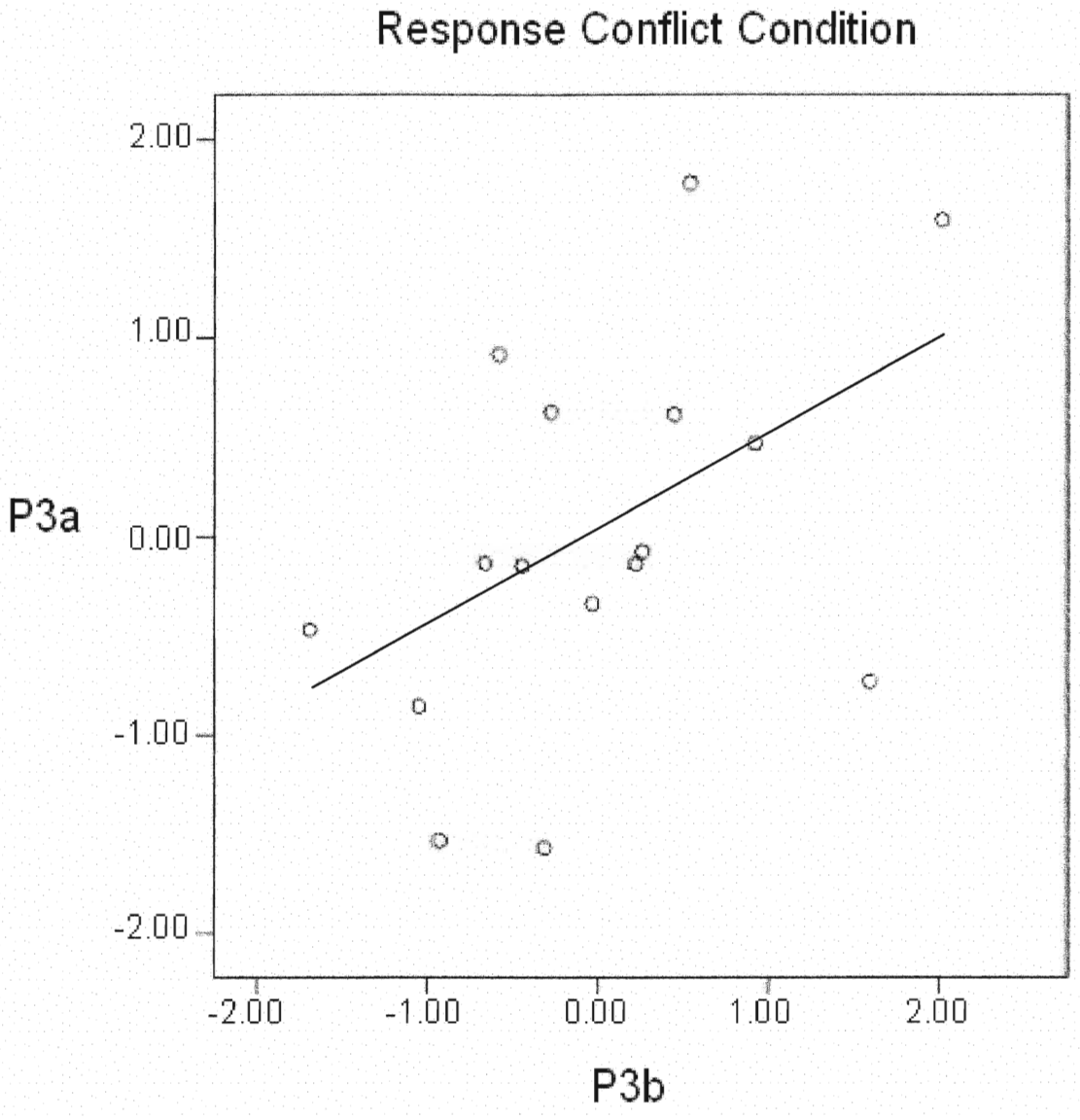


Figure 23. Scatter plot of the relationship between the P3a and P3b standardized residuals of older adults in the Positive condition (r = .487).

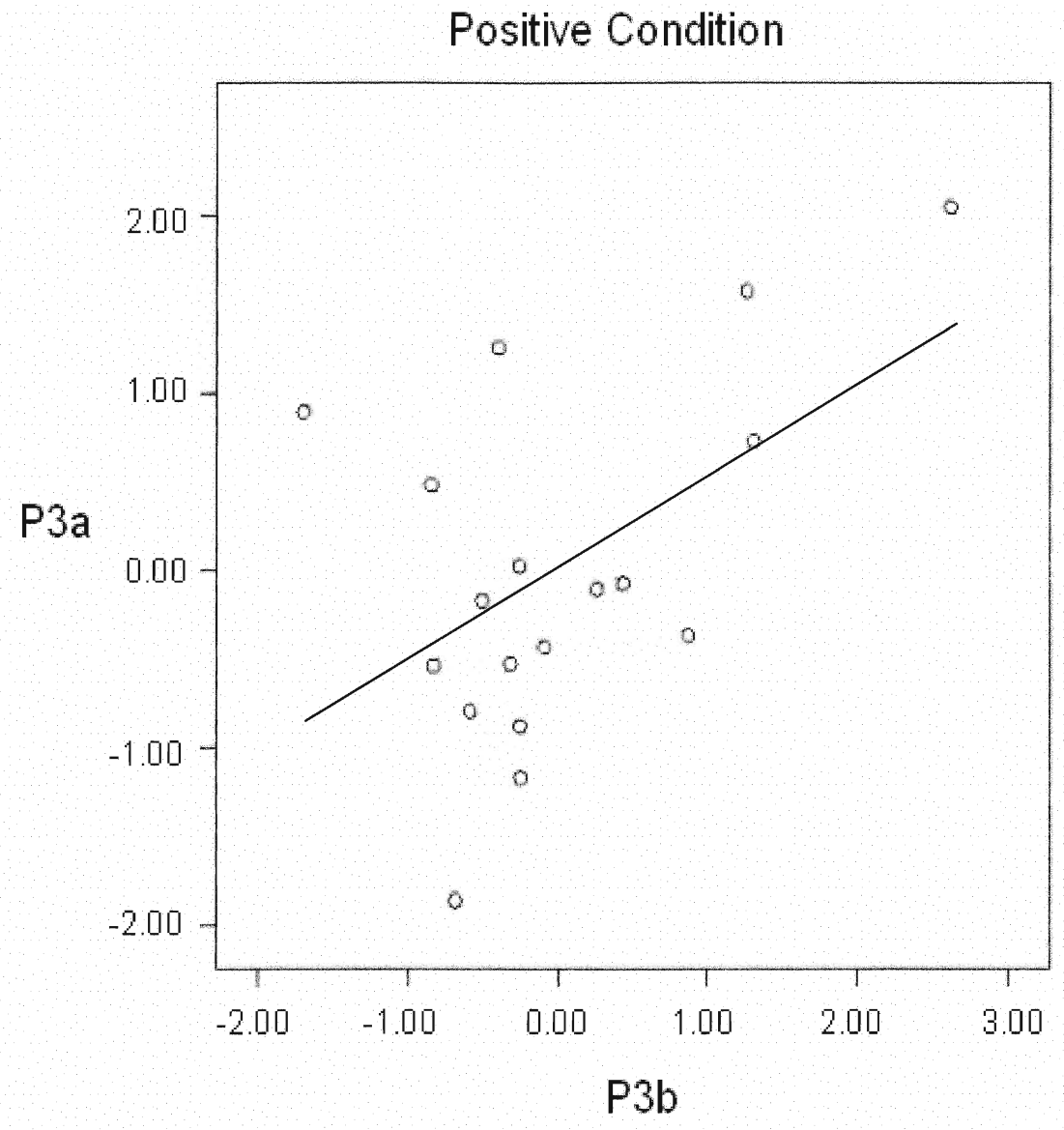


Figure 24a. Scatter plot of the relationship between the N450 and P3b standardized residuals of younger adults in the Familiar condition (r = .796).

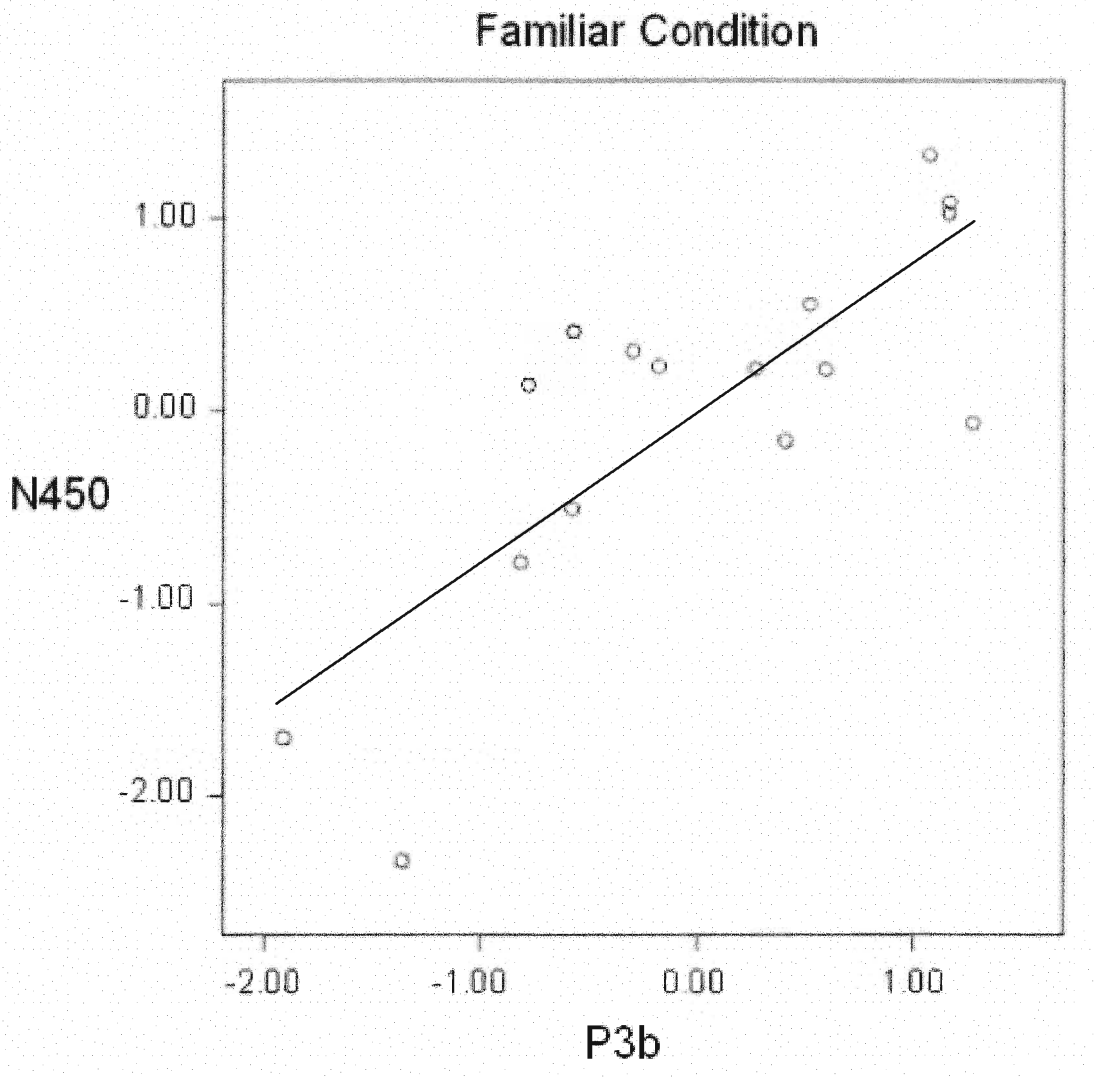


Figure 24b. Scatter plot of the relationship between the N450 and P3b standardized residuals of younger adults in Response Conflict condition (r = .731).

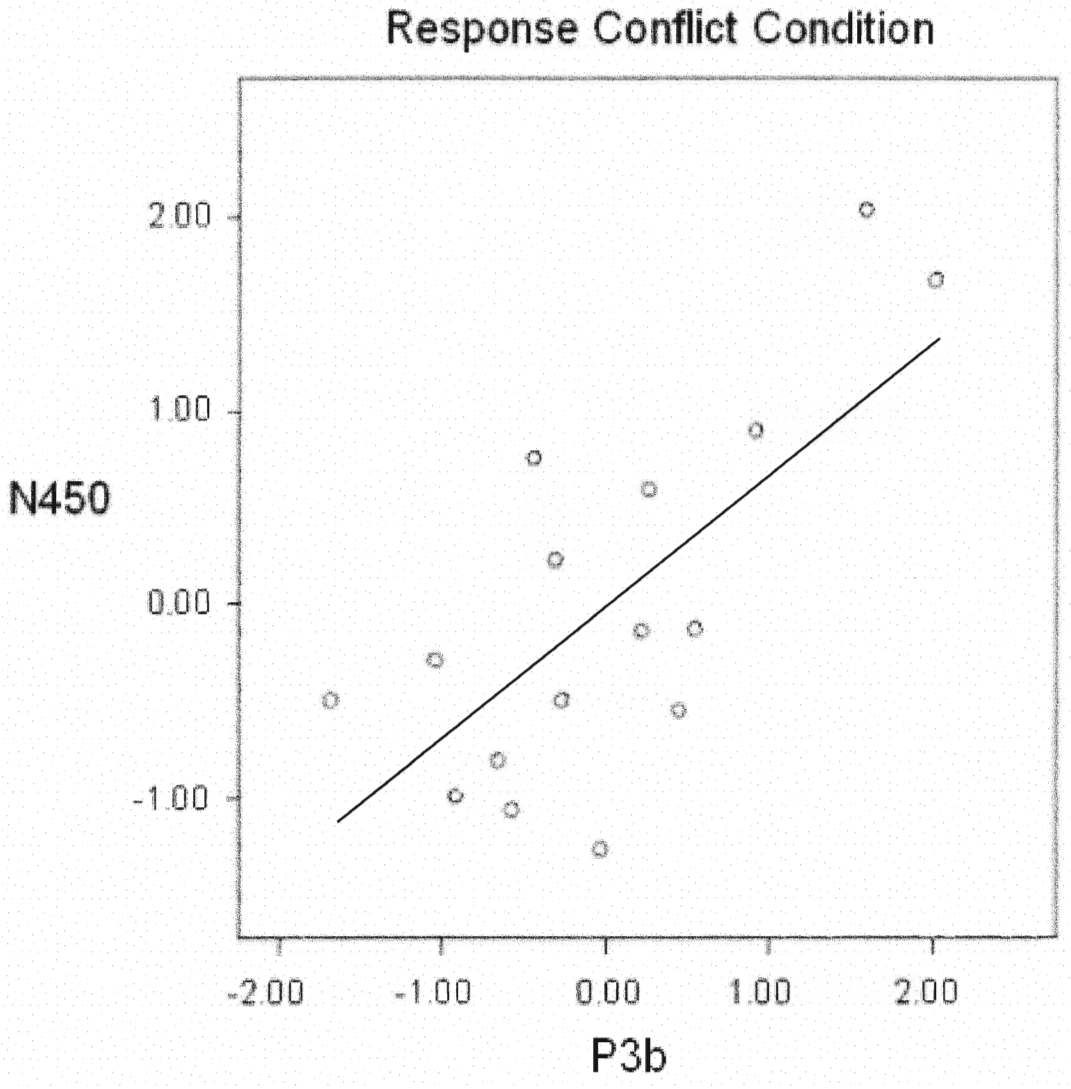


Figure 25a. Scatter plots of the relationship between the N450 and P3a standardized residuals of older adults in the familiar condition (r = .724).

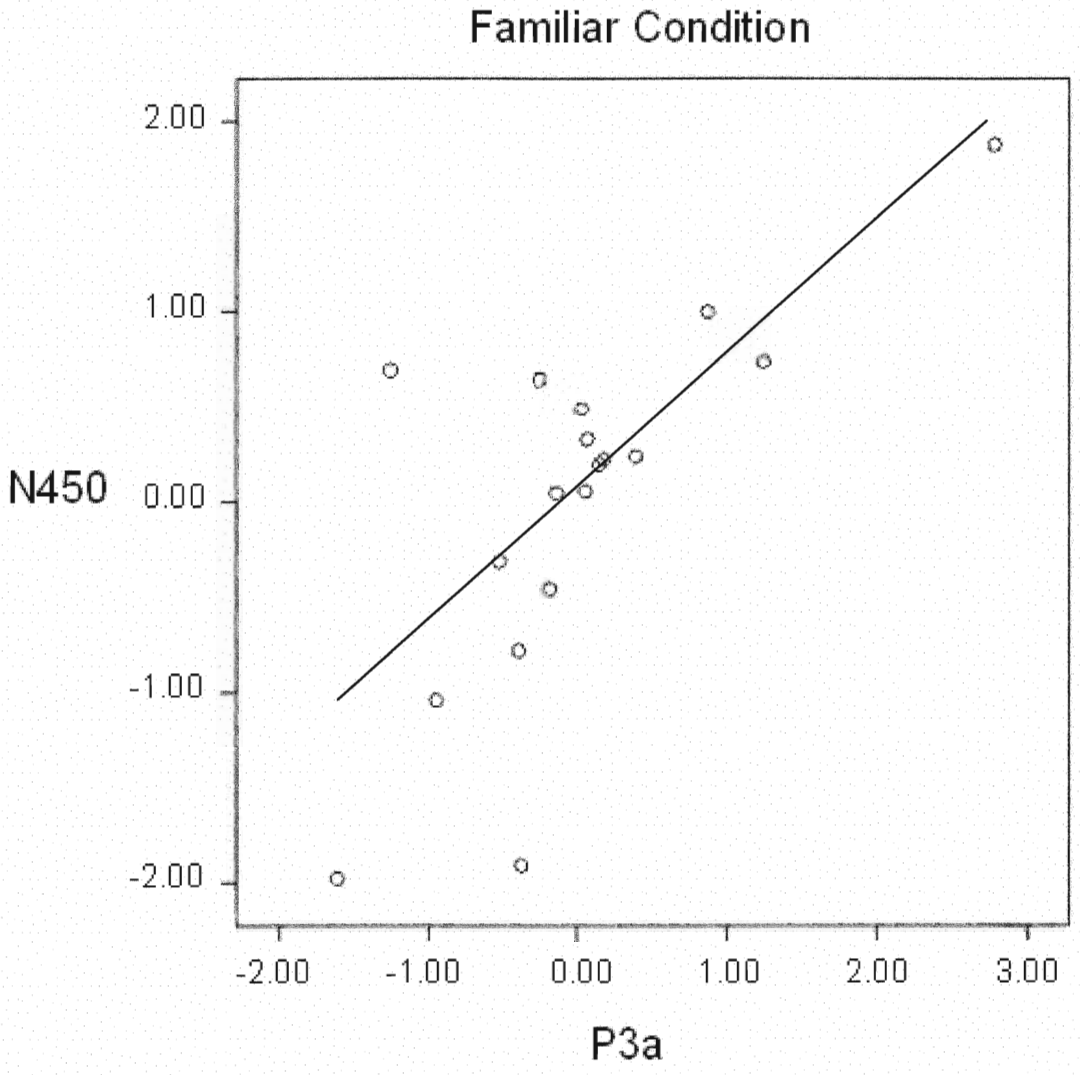


Figure 25b. Scatter plot of the relationship between the N450 and P3a standardized residuals of older adults in the Response Conflict condition (r = .520).

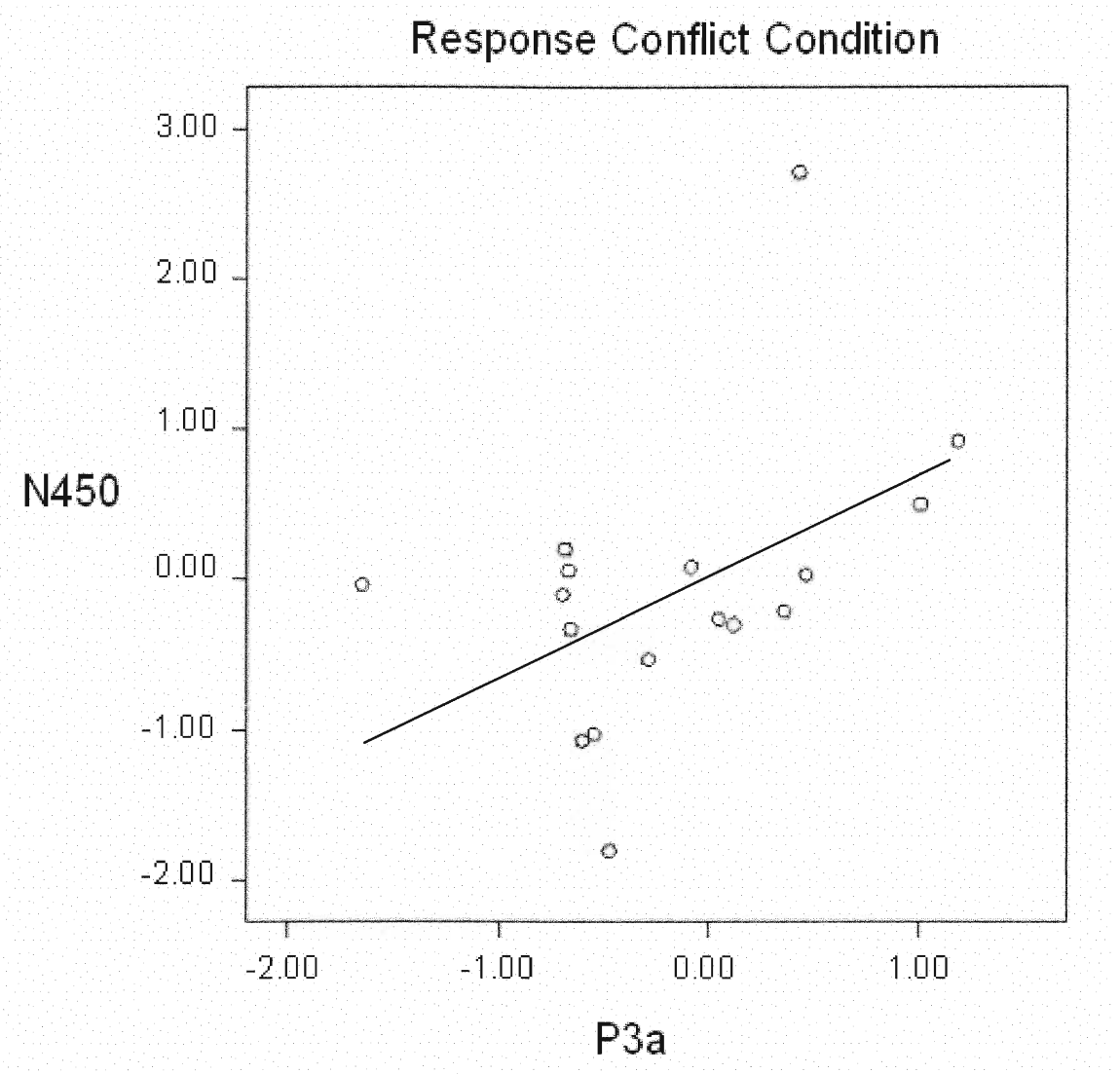
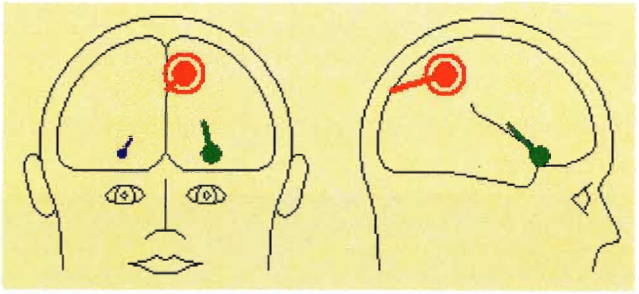


Figure 26. Placement of dipole models in the source analysis of the younger adult's condition data from 400-500 ms post-stimulus.

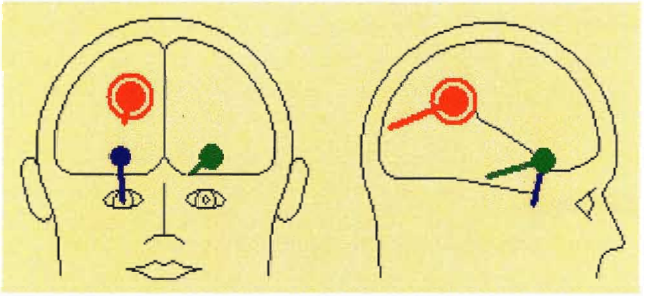
Model 1: Positive Condition



Red x = -26.9, y = -9.0, z = 75.2
Green x = -24.5, y = 51.5, z = 32.4
Blue x = 24.5, y = 51.5, z = 32.4

Residual Variance: 8.5%

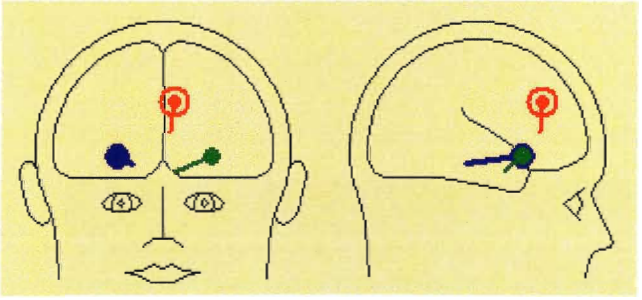
Model 2: Baseline Condition



Red x = 24.1, y = -14.7, z = 76.9
Green x = -30.5, y = 46.1, z = 26.3
Blue x = 30.5, y = 46.1, z = 26.3

Residual Variance: 11%

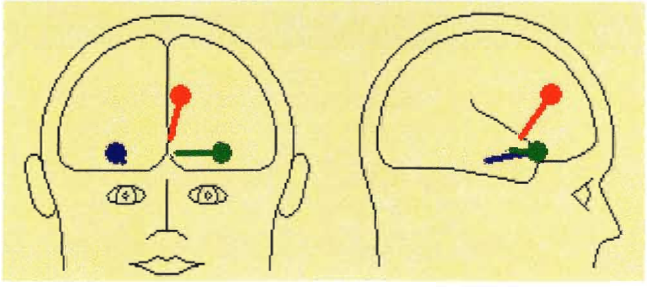
Model 3: Familiar Condition



Red x = -7.8, y = 58.2, z = 67.5
Green x = -35.9, y = 43.1, z = 26.6
Blue x = 35.9, y = 43.1, z = 26.6

Residual Variance: 15%

Model 4: Response Conflict Condition



Red x = -7.8, y = 58.2, z = 67.5
Green x = -36.3, y = 43.2, z = 26.6
Blue x = 36.3, y = 43.2, z = 26.6

Residual Variance: 12%

Appendix A

Analyzing the Topographical Variance of the N450 Component. The rationale for analyzing the topographical variance of the N450 response in both age-groups involved identifying systematic differences between younger and older adults that could have affected the ability of traditional single-site analyses in identifying the effect of condition on the N450 component. If one site was selected for analysis but the two groups showed a different pattern of clustering around this site, i.e., one group clusters tightly around the site while the other group is disparate, then the ERP component of the prior group will be better represented at this site than ERP components of the latter group. The result is that the analysis of this single site in one group will be more sensitive than the analysis of the other.

The first step to deal with this issue was to attempt to let the location of the N450 site vary for each individual in the analysis. The location of the maximal N450-like response (i.e. the point of greatest negativity occurring within the 400-500 ms time window across all frontal sites), and the amplitude at this site was used to represent a new measure of the N450 response. A mixed model ANOVA was done for these maximal N450 responses for each condition (4) and group (2). However, there were neither condition difference ($p = .45$) nor any effect of group ($p = .57$).

Although the measure of the maximal N450 response was not sensitive to condition, partly due to increased variability in the magnitude of the maximal N450 responses, the location of the maximal N450 responses was quite clearly different between groups with the younger group being more homogenous in their response than the older group. Therefore, an analysis of the variance of maximal N450 location was done to identify differences between groups and conditions. The variance

measure was created by first identifying the 3-demensional Cartesian coordinates of the site of maximal N450 response in each individual for each condition. Next the difference between the coordinates of one individual's maximal site and the location of each other individual's site (in their respective age group) was found; therefore, rendering three values, one for each Cartesian coordinate: x, y and z. These three difference scores were first squared then summed, creating a measure akin to a Cartesian vector. These scores were then divided by the number of participants in the respective age group, in order to equate for the number of individuals contributing to the squared difference measure. This rendered a single variance score for each individual in each condition presented. Group and condition averages are presented in Table 10.

Notes Regarding the Time-Window of the N450 Measure. When reviewing Figure 6b it appears that the discrete N450 activity occurring for the baseline condition may be preceding the negativity of the conflict conditions. The 400-500 ms time-window of the N450 measure may, therefore, fully capture the negativity of the conflict condition but not the baseline condition. If this is the case, then the choice of the 400-500 ms time window of the N450 may be partly confounding the results in favour of greater negativities in the conflict conditions. In order to investigate this possible confound, an analysis was done of the peak amplitudes and latencies of the N450 at site Afz21 from 300-500 ms for younger adults. The first result of this peak analysis was the observation that there were, in fact, two discrete negativities within the 300-500 ms time window. The first peak was occurring at approximately 350 ms post-stimulus while the second occurred, on average, around 425 ms post-stimulus.

This second component, which corresponded to the N450 component in the present study, was present for each condition, including the baseline condition although to a much lesser extent than the conflict conditions. The first component, the "N350", was also occurring in each condition but did not appear different in peak amplitude across the different conflict conditions. This N350 component appeared to be the source of the seemingly early N450-like component for the baseline condition in Figure 6a.

A preliminary analysis of the peak N350 revealed no significant differences between conditions in the younger group, $F(3, 45) = .89$, $p = .49$, $\omega^2 = .05$. The peak N450 measure was sensitive to condition, $F(3, 45) = 6.58$, $p = .001$, $\omega^2 = .31$, and follow-up analysis revealed significant differences between the baseline versus

familiar and response conflict conditions. This analysis supported the notion that the 400-500 ms window used in the present study was appropriate and did not confound the current findings. The analysis also supported the finding that conflict effects were present for both the familiar and response conflict condition in comparison to baseline. Although a full analysis of the peak N450 and N350 components was beyond the scope of the current study, future investigations should include this mode of analysis in order to determine the most reliable method of measuring the N450: an average area measure or a peak amplitude measure.

Appendix B:
ANOVA Summary Tables

TableB-1.
5 (Condition) x 2 (Group) Mixed ANOVA for Percent Accuracy in the Sternberg Task.

ANOVA Summary

Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	.158	4	19.75	.001	.38
C x G	.010	4	1.22	.31	.04
Error	.256	128			
Between-Subjects Effects					
Group (G)	.019	1	4.06	.052	.11
Error	.149	32			

TableB-2.
5 (Condition) x 2 (Group) Mixed ANOVA for Response Time (ms) in the Sternberg Task.

ANOVA Summary

Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	725206	4	35.60	.001	.53
C x G	17844	4	.87	.456	.03
Error	651833	128			
Between-Subjects Effects					
Group (G)	2460638	1	17.12	.000	.35
Error	4600122	32			

Table D-3.
5 (Condition) x 5 (Site) x 2 (Group) Mixed ANOVA for P200 Amplitude.

ANOVA Summary

Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	11.94	4	1.20	.36	.04
C x G	119.20	4	1.93	.11	.06
Error	318.71	128			
Site (S)	46.85	4	3.03	.032	.09
S x G	25.46	4	1.65	.198	.05
Error	494.24	128			
C x S	7.62	16	.91	.48	.03
C x S x G	18.01	16	1.12	.35	.03
Error	267.26	512			
Between-Subjects Effects					
Group (G)	8.53	1	.19	.69	.01
Error	1451.57	32			

Table D-4.
5 (Condition) x 5 (Site) x 2 (Group) Mixed ANOVA for P3a Amplitude.

ANOVA Summary

Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	25.11	4	2.69	.046	.08
C x G	28.95	4	3.11	.026	.09
Error	298.31	128			
Site (S)	310.47	4	9.79	.000	.23
S x G	121.14	4	3.82	.026	.11
Error	1014.57	128			
C x S	15.38	16	1.21	.31	.04
C x S x G	6.62	16	.51	.82	.02
Error	415.46	512			
Between-Subjects Effects					
Group (G)	62.76	1	1.58	.22	.05
Error	1270.26	32			

TableB-5.
Simple Effects Analysis of Condition in Each Age Group for P3a Amplitude.

ANOVA Summary

Source	*SS*	*df*	*F*	*p*	η^2
Young					
Condition (C)	28.82	4	3.58	.012	.19
Error	120.70	60			
Old					
Condition (C)	25.02	4	17.78	.000	.51
Error	710.34	68			

TableB-6.
5 (Condition) x 2 (Group) Mixed ANOVA for P3a Latency (ms).

	ANOVA Summary				
Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	1106.11	4	.29	.88	.01
C x G	8269.97	4	2.18	.075	.06
Error	121381.32	128			
Between-Subjects Effects					
Group (G)	188141	1	84.49	.000	.72
Error	71259	32			

Table D-7.
5 (Condition) x 5 (Site) x 2 (Group) Mixed ANOVA for P3b Amplitude.

ANOVA Summary

Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	308.82	4	3.58	.012	.10
C x G	360.55	4	4.18	.005	.12
Error	2761.25	128			
Site (S)	17088.13	4	20.87	.000	.40
S x G	16541.55	4	20.20	.000	.39
Error	26203.55	128			
C x S	748.55	16	2.34	.038	.07
C x S x G	725.00	16	2.27	.044	.07
Error	10232.19	512			
Between-Subjects Effects					
Group (G)	79.01	1	.26	.61	.01
Error	303.80	32			

TableB-8.
Simple Effects Analysis of Condition in Each Age Group for P3b Amplitude.

		ANOVA Summary			
Source	*SS*	*df*	*F*	*p*	η^2
Young					
Condition (C)	624.66	4	3.50	.012	.19
Error	2674.97	60			
Old					
Condition (C)	8.47	4	1.67	.173	.09
Error	972.04	68			

Table D-9.
4 (Condition) x 5 (Site) x 2 (Group) Mixed ANOVA for N450 Amplitude.

	ANOVA Summary				
Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	13.21	3	1.64	.185	.049
C x G	26.89	3	3.34	.022	.10
Error	257.44	96			
Site (S)	44.29	4	1.85	.180	.06
S x G	60.54	4	2.52	.111	.07
Error	766.69	128			
C x S	4.59	12	.78	.549	.02
C x S x G	1.87	12	.32	.879	.01
Error	187.78	384			
Between-Subjects Effects					
Group (G)	645.30	1	13.94	.001	.30
Error	1481.08	32			

Table D-10.
4 (Condition) x 3 (Site) x 2 (Group) Mixed ANOVA for N450 Amplitude at Lateral Sites.

	ANOVA Summary				
Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	11.11	3	1.63	.188	.05
C x G	17.24	3	2.53	.062	.07
Error	218.57	96			
Site (S)	4.82	2	.84	.423	.026
S x G	20.79	2	3.62	.039	.10
Error	183.87	64			
C x S	.78	6	.28	.904	.01
C x S x G	4.50	6	1.59	.175	.05
Error	90.37	192			
Between-Subjects Effects					
Group (G)	302.69	1	10.02	.001	.29
Error	967.56	32			

TableB-11.
4 (Condition) x 2 (Group) Mixed ANOVA for N450 Amplitude at Site Afz21.

ANOVA Summary

Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	4.68	3	1.86	.142	.06
C x G	8.41	3	3.34	.022	.10
Error	80.54	96			
Between-Subjects Effects					
Group (G)	189.18	1	17.31	.000	.35
Error	349.65	32			

TableB-12.
Simple Effects Analysis of Condition in Each Age Group for N450 Amplitude at Site Afz21.

	ANOVA Summary				
Source	*SS*	*df*	*F*	*p*	η^2
Young					
Condition (C)	11.66	3	4.16	.014	.22
Error	42.07	45			
Old					
Condition (C)	.78	3	.26	.74	.01
Error	51.06	51			

TableB-13.
4 (Condition) x 2 (Group) Mixed ANOVA for Site Variance of the Maximal N450 .

ANOVA Summary

Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	6292.39	3	5.20	.002	.14
C x G	1632.96	3	1.35	.26	.04
Error	38714.06	96			
Between-Subjects Effects					
Group (G)	5243.29	1	3.63	.066	.10
Error	46227.64	32			

TableB-14.
4 (Condition) x 2 (Group) Mixed ANOVA for an Expanded Measure of the N450.

	ANOVA Summary				
Source	*SS*	*df*	*F*	*p*	η^2
Within-Subjects Effects					
Condition (C)	7.93	3	2.31	.081	.07
C x G	10.73	3	3.12	.030	.09
Error	109.99	96			
Between-Subjects Effects					
Group (G)	92.07	1	7.74	.009	.20
Error	380.83	32			

TableB-15.
Simple Effects Analysis of Condition in Each Age Group for the Expanded N450.

	ANOVA Summary				
Source	*SS*	*df*	*F*	*p*	η^2
Young					
Condition (C)	16.67	3	3.98	.014	.21
Error	62.89	45			
Old					
Condition (C)	1.08	3	.39	.716	.02
Error	47.9	51			